Digitized by the Internet Archive
in 2007 with funding from
Microsoft Corporation

http://www.archive.org/details/physiologyofspec00greeuoft

PHYSIOLOGY OF THE SPECIAL SENSES

MPhy. G.

PHYSIOLOGY OF THE SPECIAL SENSES

BY

M. GREENWOOD, JUNR.
M.R.C.S., L.R.C.P., F.S.S.

STATISTICIAN TO THE LISTER INSTITUTE OF PREVENTIVE MEDICINE; DIRECTOR OF THE LONDON HOSPITAL STATISTICAL DEPARTMENT; LATE SENIOR DEMONSTRATOR OF PHYSIOLOGY IN THE LONDON HOSPITAL MEDICAL COLLEGE; AND EXAMINER IN PHYSIOLOGY TO THE UNIVERSITY OF ST. ANDREWS

LONDON
EDWARD ARNOLD
1910

104475
2/8/10

[All rights reserved]

PREFACE

I HOPE that this volume may be of service to two classes of readers. Students of Psychology may desire to obtain more information regarding the physiological side of the senses than is usually found in works professedly dealing with psychology. I think such students will find this book of use if they read it in conjunction with Professor Myers' admirable treatise on Experimental Psychology.[1]

Another class of readers which I have had in mind are those who are either taking up physiology as a branch of liberal education, or with a view of presenting themselves for certain higher professional examinations. In either case a somewhat more detailed knowledge of physiology is required than can be obtained from the general text-books of the subject, while time hardly permits of much use being made of original sources of information. The necessity in such cases arises for books intermediate between the text-book and the original memoir. In most branches of physiology this want is abundantly supplied, but I am not acquainted with any such aids to study in the case of the senses. This book may help to fill the gap.

The object I have had in view has compelled me to

[1] *A Text-book of Experimental Psychology*, by Dr. C. S. Myers, 8s. 6d. net (London: Edward Arnold).

restrict the work within definite limits. I have abstained from describing the anatomy and histology of the sense organs, since information on these matters is to be found in any general text-book, and I assume the reader to be acquainted with the rudiments of physiological optics and acoustics.

Bibliographical references have been confined for the most part to easily accessible works. If the reader is tempted to follow up the clues given, the ends of this book will have been completely attained.

M. GREENWOOD, JUNR.

LOUGHTON, *January* 1910.

CONTENTS

PHYSIOLOGY OF THE SPECIAL SENSES

CHAPTER I

INTRODUCTION—THE "LAWS" OF MÜLLER, WEBER, AND FECHNER

THAT province of Physiology to which has been assigned the investigation of our special sense mechanisms is of wide extent. We have to deal with the representation in consciousness of effects produced upon the bodily structures by different physical agents under conditions of the most varied nature. In some cases, the results are manifest; in others, their existence may be inferred with more or less plausibility; in yet others, although the conscious reaction, the sensation, is distinct enough, the physiological change which is associated with it eludes our imperfect means of investigation.

From very early times sense physiology and psychology have proved themselves of absorbing interest alike to philosophers and men of science, and a history of the subject if adequately treated would make an interesting record of the progress of scientific thought. In this book I can do no more than indicate very imperfectly how the workers of long ago and of to-day have endeavoured to mould their theories and observations into that organised body of knowledge which is a science.

The main problem, then, is this: Given a series of physical processes of assumed constancy, and a number of conscious states also assumed to have a real existence—from the standpoint of science as distinct from metaphysics—we have to trace out the intervening physiological processes.

It is scarcely necessary to remark that Sense Physiology has nothing to say regarding a causal link between physio-

logical changes and sensations. We are merely concerned with a time sequence, and make no attempt to bridge the gulf between the worlds of physiology and psychology.

The scope of our inquiry being so wide, it is natural to ask, first, whether there are any general formulæ, or laws, describing some relations between external stimuli and conscious reactions valid for all the sense organs. Three such formulæ have been enunciated, the "laws" of Müller, Weber, and Fechner, and we shall begin our task with an investigation of them.

The first in point, both of time and importance, is undoubtedly Müller's "law," which may be enunciated in the following terms:—

1. Different stimuli acting upon the same sense mechanism are followed by the same kind of sensation.

2. The same stimulus acting upon different sense mechanisms calls up different sensations.

This formula is often called the "Law of Specific Sense Energy," but the terminology is bad, since the word energy has acquired a meaning differing much from that in vogue when the law was first published.

In discussing this law, two phrases are employed which need definition. An "Adequate Stimulus" is that form which usually acts upon the sense organ under consideration; for instance, light is an adequate stimulus to the eye. An "Inadequate Stimulus" is one differing in kind from those generally effective; thus a blow on the eyeball is an "inadequate" stimulus for the organ of vision.

If the use of common words in uncommon senses be bad, then this terminology cannot be defended; be this as it may, in employing it one conforms to the established custom.

It is clear that the, anatomically, more complex sense organs are shielded from the possible action of inadequate stimuli; for example, the organ of hearing is not readily exposed to the incidence of light waves, and the situation of the eye guards against its mechanical stimulation. It is not, therefore, easy to test Müller's "law" in these instances, although many attempts have been made.

Nagel remarks, with justice, that the supposed proofs in

the case of sight are not convincing; the flash of light seen by an unanæsthetised patient on section of the optic nerve might well be due to mechanical stimulation of the retina, and a similar objection can be urged against other like experiments. The most elegant illustration of the law is afforded by the results of stimulating the central end of the chorda tympani, chemical, mechanical and thermal excitation alike calling up a sensation of taste. The reader will of course notice that this is not a proof, but an illustration; inadequate stimulation of the supposed end organs of taste themselves has not led to very definite results.

Although we have no rigorous proof of the correctness of Müller's "law," the formula is of real scientific value. As we shall see, many early thinkers were hampered in their speculations by an axiom dating back to remote ages which asserts that "causes" and "effects" are necessarily *similar* in a narrow sense. Müller was, perhaps, the first physiologist definitely to abandon this ancient and sterile dogma, his "law" defining accurately the modern point of view in discussion of this type.[1]

The next formula, Weber's "law," carries into the province of experimental psychology, and another definition of terms is required. If corresponding to a stimulus of given intensity A we experience a sensation of "magnitude" B (*vide infra*), then if the stimulus be increased or diminished very slightly no difference in the sensation will be experienced. When, however, the increase or decrease exceeds a certain limit, the intensity of the sensation changes. Again, if a stimulus be increased in intensity from nothing, only after a certain point has been reached will any sensation be experienced. The absolute magnitude of the stimulus in the second case, and the difference of the magnitudes in the first case, measure the *threshold* or *liminal* values, and may be alluded to as threshold or liminal stimuli.

For information as to the manner in which such experiments are carried out, together with details as to possible sources of error, the reader must consult special works; space

[1] See Helmholtz, *Handb. d. Phys. Optik. 2te. Aufl.*, pp. 248, etc.

only permits of a short note as to the leading principles involved.

Most methods of experiment fall under one of the three following groups :—

(1) The Method of Smallest Perceptible Differences.

This simply consists of passing from one intensity of stimulus, by small increments, to the just noticeable next "higher" sensation. Most of Weber's own work was carried out in this way.

(2) The Method of Right and Wrong Answers.

Two stimuli, A and B, are chosen of nearly equal magnitudes, *e.g.* a pair of weights. The subject is then asked which is heavier, his answer recorded, and the experiment repeated many times.

If the number of correct answers be only about equal to the number of incorrect ones, it is concluded that the difference between the two stimuli is inappreciable. The experiments are then repeated with weights differing by a greater amount, values being finally reached for which the number of correct judgments definitely exceeds—when tested by an adequate statistical process—the number of incorrect ones; it is inferred that at this stage a definite subjective appreciation of the difference has been attained.

(3) The Method of the Mean Error.

Using the former illustration, a subject is asked to choose from a large number of weights all those exactly equal to a standard. All the weights he chooses will not be exactly equal; the differences from the standard are recorded,[1] and their sum, divided by the total number of trials, is thought to give the average error the subject may be expected to make. This magnitude will be a lower limit for the threshold value.

It may be said at once that results obtained by the employment of any of these methods require the use of most refined statistical reasoning before any importance whatever can be attached to them, and such an analysis has not always been forthcoming.

As a result of investigations of this kind, carried out by Weber, Fechner, and others, the following conclusions were

[1] Without regard to sign.

reached:—The just noticeable increase of a stimulus bears a constant ratio to the original stimulus, or, two stimuli in order to be discriminated must be in a constant ratio, the latter being independent of the absolute magnitudes of the stimuli. The actual value of this ratio, although constant for any one sense mechanism, varies from organ to organ. This is Weber's well-known "law."

Accepting Weber's "law" as true, an attempt was made by Fechner to express sensations in terms of quantitative units. Having adopted certain assumptions of which the most important perhaps is, that all just noticeable differences of sensation contain an equal number of sensation-units, it was easy to deduce from Weber's "law"[1] that the sensation varies as the logarithm of the stimulus. This corollary is Fechner's "law."

The validity of Weber's "law" and Fechner's corollary have been hotly contested. The problem is complex, and little is gained by either confident abuse[2] or praise. The following remarks, which agree essentially with v. Kries' opinions,[3] indicate some of the more important difficulties in the way of accepting Fechner's conclusions.

Experimental methods of measuring threshold stimulus values are open to criticism from both the theoretical and practical standpoints. The theoretical objections are intimately associated with certain deductions from the theory of correlation, and cannot be examined here. A practical difficulty is the tacit assumption that the perceptive mechanism of the person who is the subject of our experiments is a constant factor throughout a series of observations. This is not, however, true. What is a just noticeable stimulus at

[1] The simplest way of putting it is: If E be the measure of a sensation and dE a liminal increment, R the measure of a stimulus and dR a small increment, then

$$K \frac{dR}{R} = dE, \text{ where K is a constant (Weber's law),}$$

hence

$$\int K \frac{dR}{R} = E,$$

or $K \log_e R + K_1 = E$ (Fechner's law).

[2] Such, for example, as will be found in Prof. W. James's *Principles of Psychology*, vol. i. pp. 548–9.

[3] See particularly "Zur Psychologie der Sinne," Nagel's *Handb. d. Physiol. d. Menschen*, vol. iii. pp. 16, etc.

one time may be inappreciable at another, owing to a change, physiological or psychological, in this factor. A higher threshold value is often observed when we proceed from a weaker to a stronger stimulus than in following the reverse order. It follows that the experimental methods employed to establish Weber's "law" may yield, and do yield, inconstant results, and a system of measurements which gives different readings when operating through the same range is of little service.

It has also been shown that even under favourable conditions the formula is definitely invalid for very weak or very strong stimuli.

We seem, therefore, forced to conclude that the experimental basis of Weber's "law" is not firm enough to permit our attaching much importance to the formula itself.

These objections are directed to the *form* Weber's "law" takes: that *some* relation of this kind exists is probable, for all judgments involve comparison; but it may well be doubted whether the present state of knowledge permits any more definite assertion.

If the conclusions just stated be sound, Fechner's corollary evidently fails, but, over and above this, special objections to it can be assigned. For instance, Fechner's "law" assumes that sensations are quantitatively measurable, and this is, to say the least, not self-evidently true. Measurements only have a meaning when the unit is clearly and uniquely defined, or, under very special circumstances only, when its existence can be inferred. Changes of temperature could be measured in various ways, and to say that the temperature of A is 1 degree higher than that of B conveys a definite idea to the mind of him who realises that the scale of units is fixed and has a constant physical significance.

In the case of sensations, no such scale has been given.[1] To say that one body has twice the mass of another is intelligible, because the unit of mass can be defined;[2]

[1] See in this connection Lloyd Morgan's Croonian Lecture, *Proc. Roy. Soc.*, vol. lxviii. p. 459.

[2] Even in such a case the definition is not particularly easy; the reader should consult *La Science et l'Hypothèse*, by H. Poincaré, chap. viii.

to say that one sensation is twice as intense as another means nothing until the unit is fixed. It seems doubtful, then, whether we are in a position to measure sensations at all, and until we are, the formulation of a quantitative law is hardly justifiable.

Some of these points may come up for consideration once more in connection with the various organs, but it is well to note from the outset that the numerous statements which have been made with regard to the sense organs in general are liable to very real objections. We are not yet in sight of that simple, all-embracing formula to supply which is the aim of science.[1]

BOOKS AND PAPERS RECOMMENDED FOR FURTHER STUDY

(Bibliographical references under this heading are intended to help students desiring to pursue the subject further. They are invariably confined to works readily accessible in a moderately good library.)

Müller's Law

W. Nagel, Die Lehre von den Spezifischen Sinnesenergien, Handb. d. Physiol. d. Menschen, herausgegeben von W. Nagel, vol. iii. pp. 1–15.

L. Asher, Das Gesetz der Spezifischen Sinnesenergie und seine Beziehung zur Entwickslungslehre, Zeitsch. f. Psychologie und Physiologie der Sinnesorgane, 1906, vol. xli. p. 157 (this journal will be denoted in future by the letters Z.P.P.S.O.).

Weber's and Fechner's Laws

J. v. Kries, op. cit. (a thoughtful and instructive criticism).

G. F. Lipps, Grundriss der Psychophysik, Leipzig, Sammlung Göschen, 1903. An elementary account from the psycho-physical standpoint.

G. E. Müller, Die Gesichtspunkte und die Tatsachen der psychophysischen Methodik, Ergebnisse d. Physiologie, zweiter Jahrgang, 1903, second part, pp. 267–517. (A very full, and somewhat difficult account, with complete bibliography of modern psycho-physical literature.)

Professor James's remarks can be read with pleasure (*op. cit.*), although his criticism does not appear adequate.

---

[1] It is not of course implied that to assume a quantitative relation between stimulation *processes* and sensation *processes* is necessarily illegitimate. In fact, as will appear later, such an assumption often leads to extremely useful working hypotheses; the student ought, however, to realise what caution the proceeding requires.

CHAPTER II

GENERAL PHYSIOLOGY OF CUTANEOUS SENSATION

In studying any branch of knowledge it is an obvious advantage to begin with its simplest and most readily intelligible manifestations, and to approach only by gradual stages its more complex parts. In most cases this plan can be readily followed, but in sense physiology peculiar difficulties are encountered. To judge from the number of pages allotted in a general text-book to the sense organs of the skin, on the one hand, and to the eye, on the other, it might be supposed that the physiology of the former is much easier than that of the latter. Such is by no means the case; in fact, the converse proposition is quite arguable. At the same time, the study of cutaneous sensation is in many respects peculiarly instructive, and it will therefore be convenient to undertake it at once.

At the outset we shall see that the tendency of modern workers has been to conceive of the cutaneous surface as a universe of points, each reacting in a specific manner to the application of stimuli. We shall study the results which have led up to this, and then examine important modifications of the conception which have been rendered necessary by more recent discoveries.

Pre-Aristotelian writings on cutaneous sensations are too vague to be of service to the modern reader. The scientific history of the subject really commences with Aristotle.[1]

Aristotle recognised distinctly that the sense of "touch" is separable into many sense modalities, although his limited means of investigation did not permit him to render the

[1] For information as to Greek Sense Physiology the reader is strongly advised to consult Professor J. I. Beare's admirable work, *Greek Theories of Elementary Cognition from Alcmæon to Aristotle.* Clarendon Press, 1906.

distinctions precise. He also anticipated the view that the organs are affected by a *change* of state. He regarded the sense of touch as fundamental, and the only one necessary to existence.

In both these conclusions Aristotle has been followed by the majority of subsequent writers. Without attempting to detail the course of investigations which have led up to the modern epoch, I shall describe in as few words as possible the state of knowledge gained up to a few years ago.

At least four distinct qualities of sensation can be distinguished when stimuli are applied to the skin—those of touch or pressure, warmth, cold, and pain. Some writers have advocated an even finer analysis, regarding, for instance, the sensation of itching as specific, but this is hardly warranted by experiment. It is quite clear that a series of points can be mapped out over the skin, stimulation of which produces the sensations of heat, cold, pain, and touch; the question of pain, however, will occupy us subsequently. The principles of experimental methods for this sort of work are simple enough, although the actual instruments vary enormously in detail. For experimenting on tactile perception, v. Frey, who has done pioneer work in cutaneous sense physiology, devised a series of valuable instruments.[1] They consist of a number of wooden rods, to the ends of which hairs of differing thickness are fixed at right angles. If the hair be applied perpendicularly to a point on the skin and pressure exerted, then with the application of a certain pressure the hair will be visibly bent. The amount of pressure required to bend visibly any given hair can be experimentally determined, and with a large series of hairs of different thickness we can use pressures measured and graded with some accuracy.

Toulouse and Vaschide have justly remarked[2] that different readings will be given with the same hair unless the pressure is arrested at the instant of bending, a point not

[1] Bloch described a similar but less perfect instrument in 1891 (*Arch. de Phys.*, Avril 1891).

[2] Toulouse, Vaschide, and Piéron, *Technique de Psychologie Expérimentale*, Paris, 1904, p. 64.

easy to determine with absolute precision. I also think that the degree of moisture in the air makes some difference. Notwithstanding these and certain other objections, the method seems the most accurate at present in use. To study temperature sensations, a hollow pencil-shaped rod through which water at a definite temperature can be circulated is the best, although French workers claim to have obtained good results by using minute drops of water at various temperatures as stimuli.

The topography of sensation points was first completely worked out by Magnus Blix, and his conclusions have been endorsed by the best modern observers (Sommer).

These conclusions are:—

(1) Pressure points are closely related to the distribution of hairs, each hair having a pressure point near its site of eruption (v. Frey), the point corresponding on the surface to the situation of a hair follicle. There may, however, be some pressure points which do not correspond to hairs.

(2) Cold reacting points are more numerous than warm points, Sommer finding 12–13 cold points sq. cm. against 1–2 warm points, but the distribution is by no means uniform.

Respecting the anatomical structures which correspond to the sense points, hardly anything is certainly known. For instance, it is not easy to tell whether any given nerve fibre conveys centripetal or centrifugal impulses, the ordinary methods of determining the matter being generally impossible of application. The relation of pressure points to hairs renders it probable that the nerve fibre entering the root sheath and forming ring-like arborisations round the upper part of the follicle are especially associated with the pressure sense.

It is also possible that the Meissner corpuscles are pressure end organs, and may even, in the hairless parts of the skin, replace the hairs.[1]

It has been stated that Krause's end bulbs and Ruffini's organs are associated respectively with sensations of cold and warmth, but experimental evidence is of the slenderest.

[1] V. Frey, *Beiträge z. Sinnesphys d. Haut, König. Sächs. Gesellschaft d. Wissensch.*, März 1895.

Also blood supply see
The Sensory Activities of the Skin for Touch & Temperature
Edward Waterston. Brain 1923 vol XLVI p 200

Sensations of pressure can normally be evoked from the whole cutaneous surface, the mucous membrane of the mouth, the tongue, teeth, and nares. Respecting the cornea and glans penis much difference of opinion has existed, but the reason probably may be sought in a failure to distinguish the exact forms of stimuli employed, as will be clear subsequently.

Strümpell has recently[1] asserted that sensations of pressure can be set up in internal parts, tendons, fasciæ, muscles, and periosteum. Thunberg[2] has suggested that in this case tactile impressions are confused with those of pain.

The adequate (*vide supra*) stimulus for the sense of pressure is of course mechanical, but since any stimulus applied to the surface does not operate directly upon the end organs —if such there be—the question arises as to what physical conditions in the immediate vicinity of the possibly recipient structures give rise to sensations of pressure.

This problem was solved by v. Frey and Kiesow[3] in 1899. When a point, *e.g.* the end of a hair, is pushed against the skin, the pressure is greatest at the part immediately in contact with the point, and diminished in the deeper and lateral regions; that is to say, there is a fall of pressure from without inwards. Conversely, if a small plate be affixed to the skin and traction made upon it, the pressure is least externally, and increases from without inwards. In the first case we have a negative and in the second a positive slope of pressure from without inwards. V. Frey and Kiesow found that the sensations experienced in the two cases appeared to be identical, provided the magnitude of the pull in one case were equal to that of the push in the other; that is to say, the end organ is excited by a change in the existing pressure relations of end organ and superficies, whether the change be positive or negative, increase or decrease.

Although the variation in pressure in the neighbourhood

[1] *Deutsche med. Wochen.*, 1904, pp. 1411 and 1460.

[2] Nagel's *Handb. d. Phys. d. Menschen*, vol. iii. p. 657.

[3] *Z.P.P.S.O.*, vol. xx. pp. 126, etc., especially p. 153. Those desirous of experimenting on the skin should note the cautions given in this paper.

of an end organ is an essential condition for the latter's excitation, other factors modify the result.

For instance, if the stimulus be a falling weight, its velocity is a factor. The greater the velocity, within limits, the less the weight required to produce a just noticeable sensation.

The sensation does not, however, vary as the kinetic energy of the exciting mass. Two weights allowed to drop from heights inversely proportional to their masses would possess equal amounts of kinetic energy on reaching the skin, but the smaller weight produces the more intense sensation.

The extent of surface to which the stimulus is applied is also an important matter. It might be thought that the sensations excited in two areas would be identical if the pressure per unit of surface were the same in both cases. This is not so if, for instance, an area of ·5 sq. mm. be compared with one of ·25 sq. mm.; a greater pressure per unit is required in the second than in the first case to produce a just noticeable sensation. The optimum surface is approximately ·5 sq. mm.; as we increase or decrease the extent of surface stimulated from these dimensions, the liminal value increases (v. Frey and Kiesow, *op. cit.*). A partial explanation is found in the above-mentioned fact, that pressure sensations are excited by a slope of pressure from the point of application to the end organs. The greater the surface pressed upon, the less steep the slope from within outwards owing to lateral thrusts. This does not account for the fact that if the surface be *diminished* below a certain value the pressure must be increased, and the proposed solutions of the problem seem hardly adequate.

The above-mentioned experiments were made on hairless portions of the skin; the conclusions, however, are, with some modification, valid for hair-clothed surfaces.

The tactile apparatus of the hairy skin is more excitable and more readily fatigued than that of the smooth areas. Stimuli not distinguishable on a smooth can be detected if applied to a hairy surface. This lowering of the magnitude of a threshold stimulus in the hairy regions perhaps depends

on two factors,[1] the diminution of the skin area stimulated, since the pressure is only effective through the base of the hair follicle, and the lever-like action of the hair itself.

The comparison and discrimination of two pressure stimuli have been the objects of many investigations. The quantitative results are discordant, but the following conclusion appears to be well founded.

It is easier to compare weights applied successively than when they act simultaneously; *i.e.* a more accurate comparison can be made between the memory of a sensation and an actual sensation than between simultaneous sensations (Weber).

Again, the rapidity with which stimuli operate influences one's powers of discrimination. Generally, the slower the rate of change, the higher the liminal stimulus value (Dohrn).

It is also easier to perceive that a given weight differs from another than to say whether it is heavier or lighter. When such discrimination is possible, it is easier to detect an increase in weight than a decrease. If successive weights be applied with a rapidity such that, in equal times, the same fractions of the original weights are added, the ratios of increase of stimulus to original stimulus give results in fair accordance with Weber's law. It has, however, been shown (Seashore, Hall, and Motora) that the results are variable with the experimental conditions, and no definite proof of the law as applied to tactile impressions is forthcoming.

Experiments performed with the object of determining what frequency of pressure stimuli gives a fused sensation have yielded most discordant results,[2] and need not be discussed. The length of time the sensation persists after removal of the stimulating body depends on the skin area; in some places the sensation vanishes at once, in others, *e.g.* the forehead, the after-effect may with moderately strong stimuli persist some little time.

[1] Aubert and Kammler, *Pflüger's Arch.*, vol. lix. 601.

[2] Sergi, *Z.P.P.S.O.*, iii. 179; v. Kries and Auerbach, *Du Bois Reym. Arch.*, 1889; v. Vintschgau and Dürig, *Pfl. Arch.*, lxix. 377.

These, then, are the "classical" results of investigations on the sense of touch, and we can pass to those dealing with the temperature senses.

Sensations of temperature can be elicited from the whole cutaneous surface—the skin of the external ear, parts of the nasal cavity, inclusive of the anterior nares, and the mucous lining of the beginning and end of the digestive tract. There are differences of opinion as to whether such sensibility exists in the cornea, conjunctiva, and glans penis;[1] we shall see in a later chapter how it is that confusion has existed on this point. There has been much dispute as to what constitutes the adequate stimulus of the temperature end organs, two theories, those of Weber and Hering having been favoured at different times.

Weber supposed that a temperature sensation was dependent upon an alteration in the existing end organ temperature; thus a rise of temperature in the heat end organ produces a sensation of warmth, and a fall in the temperature of the cold end organ one of cold. In either case such a change could be brought about in four ways. Thus a sensation of warmth might be produced by: (1) A diminution in heat loss with a constant influx of heat; (2) a constant heat loss and increased influx of heat; (3) increased heat loss combined with a proportionately greater influx of heat; (4) diminished heat loss and heat influx, the former diminution being the more considerable.

It has been shown that whichever of these conditions be fulfilled, the sensation is the same.

It is further known that, within certain limits, given a constant external temperature sensations originally present disappear, a constant rate of heat influx and efflux being presumably established.

These facts agree with Weber's hypothesis, but certain experiments seemed difficult to reconcile with it. If a metal disc at 2° C. be applied to the forehead for 30 seconds, the sensation of cold persists for some 20 seconds after removal of the stimulus, that is, while the heat loss is diminished and

[1] See Thunberg, *op. cit.*, p. 670.

the temperature of the end organs actually rising. Hering accordingly proposed a different theory.

When a certain skin area gives us no temperature sensations, the end organs are to be regarded as being at the physiological zero of temperature. Any alteration in the thermal condition will give rise to a sensation, the intensity of which will depend on the difference from this physiological point of reference. The actual situation of the physiological zero point is presumed to vary within tolerably wide limits, not being the same for all skin surfaces, nor for the same skin surface at different times.

On entering a warm room a sensation of warmth is elicited, because the physiological thermometer is set for a lower point; but if the stay be prolonged, the physiological zero is readjusted to a higher level, and the temperature sensations disappear.

The difference between the theories is that Weber supposes sensations to arise during variation, Hering when the end organ temperature is constant.

Holm seems to have demonstrated that, if precautions be taken to prevent the spread of stimulation beyond the point originally involved, the sensation only persists for a short time after withdrawal of the stimulus, the time being so short as to correspond to the probable time during which the end organ temperature varies. The same investigator studied the experiment alluded to before, in which, after application of a cold piece of metal to the forehead, the sensation of cold persisted for some time after removal of the stimulus. Holm noticed that a distinct interval separates the appearance of the cold after-sensation from that at first experienced, and suggested that we are here dealing with a case of paradoxical sensation, that the cold end organs are stimulated by the warm blood which arrives in increasing amount owing to vasrodilatation, and that they respond specifically with a sensation of cold. The existence of such paradoxical sensations has long been known (Strümpell, Alrutz, Thunberg, and others).

Holm also found that after-sensations of cold do not follow the application of moderately intense stimuli, but only

that of strong ones. It may therefore be said that the experiment is too complex to be regarded as decisively negativing the theory of Weber, and that it is still questionable which of the hypotheses is to be preferred.

With respect to the factors which influence the threshold value of temperature stimuli, the following may be enumerated as the most important:—

(1) Situation of the point stimulated; warm and cold points are by no means uniformly distributed over the body surface. For instance, Goldscheider[1] found that cold points were far more numerous over the extremities than warm points. This author's methods have been adversely criticised, and there is no doubt that the topography recorded by different investigators is highly variable. I believe the inconstancy is partly due to real variation in the distribution of end organs, and partly to inexact methods of study.

(2) The actual size of the region stimulated. Thus Weber asserted that water at 29·5° Réaumur feels warmer than water at 32° R. if the whole hand be dipped into the former and only one finger into the latter. At the same time it is to be remembered that the considerations enumerated under (1) may account for Weber's result. It is difficult to plan an experiment in which these sources of error are avoided.

(3) The physical condition of the stimulating body, its thermal capacity, conductivity, and more or less perfect application to the skin, are important, and play their part in the divergent results noted under (1).

Finally, it may be said that the numerous researches, dating back to the middle of the last century, in which the discrimination of temperature differences has been studied, have not yielded constant enough results to demand special attention in an elementary work. Attempts to establish the validity of Weber's law in the case of temperature sensations have not been successful.

[1] *Arch. f. Psychiatrie und Nervenkr.*, xviii. 659.

BOOKS RECOMMENDED FOR FURTHER STUDY

An excellent account of modern work on the subject will be found in Professor Thunberg's article (Nagel's Handb. d. Phys., Bd. iii. p. 647). Of the original papers, those by v. Frey should be read first.

A valuable discussion of the experimental methods of dealing with the subject is contained in chapter i. of "The Grouping of Afferent Impulses within the Spinal Cord," by H. Head and T. Thompson (Brain, for 1906, part cxvi.).

CHAPTER III

PAIN

Although what is commonly termed pain is not exclusively associated with cutaneous stimulation, it will be found that the matter is best considered at this point. The discussion must be brief, since most of the problems which arise belong rather to the psychology than the physiology of the sense organs.

Many definitions of pain have been proposed by various writers, of which the following examples will suffice :—

"Pain is a change of sensibility repugnant to him who experiences it" (Mantegazza).

"Pain is any disagreeable sensation (sensation pénible) perceived by the nervous centres, but varied in its modalities, effects, and causes (Eloy).

"A sensation such that one does not desire to experience it afresh" (C. Richet).

While it must be allowed that it is not an easy task to construct a satisfactory definition of pain, it appears that the authors cited confuse what should, if possible, be kept distinct. But little reflection is necessary to convince the reader that a sensation may be unpleasant, may be repugnant in the highest degree, without falling under the category which includes, for instance, the sensation experienced when a needle is thrust into the skin.

The extraction of a tooth without gas is a disagreeable experience, and so is the death of a friend, but it is surely an abuse of language to employ the word pain indifferently for the sensory phenomena associated with such disparate causes.

We have here an example of the "fallacy of words," discussed by Bentham and other logicians. German writers have attempted to remedy this evil by using the terms

"Unlust" and "Schmerz." Any excessive stimulation of an afferent system is associated with "Unlust," and the word can also be made to cover what popular English writers convey by the phrase mental or moral pain. It is, however, true that many authors use "Schmerz" almost as loosely as "pain" or "douleur." Indeed, however one may strive for accuracy, the difficulties seem almost insuperable. Although there is fairly good evidence that the sensation associated with stimulation of the skin by a sharp instrument, such as a needle, is *sui generis* and dependent on the existence of specific organs, yet no absolute distinction can be drawn between this and the "pain" of visceral disease.

I think therefore, although it is a frank confession of weakness, that it will be convenient to use the word pain without a qualifying adjective somewhat in the sense of "Unlust," while I shall speak of the sensation which appears to have a specific basis as cutaneous pain. I am not at all clear how far visceral pain is or can be separated from "Unlust."

Funcke appears to have been among the first physiologists actually to advance the opinion that cutaneous pain is distinguishable from other afferent impressions arising from the skin. He suggested that the separation might occur first in the spinal cord, or that the impulses are insulated throughout their whole course from periphery to sensorium. The researches of v. Frey made it possible to render these ideas more precise. It was found that by the employment of suitable mechanical stimuli clearly defined points not generally coincident with the touch spots could be mapped out which yielded maximal sensations of pain. In the ordinary way it is not possible to induce a sensation of cutaneous pain entirely free from one of touch, but this can be done if only very sharp needles or bristles are used and the epidermis is moistened.

From such experiments, and from the further observation that the points would also respond to chemical stimuli by sensations of cutaneous pain, it was possible to conclude that specific organs for cutaneous pain exist. The "pain points" are characterised by a very long latent period when subjected to weak stimulation, and a special inactivity of response to

rapidly alternating or oscillating stimuli. They do not coincide with pressure points, than which they are at least four times more numerous.

The belief that cutaneous pain was induced by direct stimulation of nerve fibres, is contradicted by the fact that it can be elicited by the employment of stimuli too weak to act as ordinary nerve excitants. Further, weak mechanical stimuli, just above the liminal value, provoke a delayed sensation of pain, the delay being greater than can be accounted by the time required for the conduction of an impulse to the spinal cord, and greater than the interval which separates stimulus and response when the former is applied directly to a nerve fibre.

Although the interpretation of these experiments is more dubious than some think, they are not inconsistent with the hypothesis of specific organs for cutaneous pain. V. Frey suggests that the free nerve endings of the skin are the organs in question, and the following confirmatory evidence is adduced :—

(1) Diminution of the surface area stimulated does not diminish the effectiveness of the stimulus.

(2) The liminal value of an electrical stimulus is lower than that of any other form.

(3) Corrosives produce, first of all, a sensation of pain.

These facts suggest that the pain end organs are more superficial than those of touch or temperature. The only nervous elements definitely superficial to the end bulbs *supposed* to be associated with touch are the free intra-epithelial nerve endings, hence they should be the required organs.

It has also been asserted that, in the cornea, the only receptive elements are the intra-epithelial nerve endings, and that from the cornea painful sensations alone can be elicited. V. Frey suggests that the actual excitant might be fluid squeezed from the cells into the inter-cellular spaces. Such fluid not being sufficiently concentrated owing to the impermeability of the cell wall for certain salts, its low concentration may render it a chemical stimulus for the nerve endings. Apart from other objections which can be raised,

it should be noticed that Donaldson finds sensations other than those of cutaneous pain can be derived from the cornea.

I have already remarked on the confusion which has existed respecting the meaning of the word pain. Even with respect to cutaneous pain, as above defined, there is room for further specialisation. Thunberg, for instance, seems to hold the view that aching and stabbing or pricking (cutaneous) pains depend on totally different mechanisms. He points out that on pinching up a large fold on skin, pressure, however slight, elicits a sensation of aching pain alone, while the application of superficial stimuli under normal circumstances excites only pricking sensations. Thunberg has not, however, shown satisfactorily that the difference of sensation may not be related to the very different stimuli employed and their conditions of application.

A few notes on visceral pain my fitly be introduced at this stage. It was formerly believed that the viscera are insensitive under normal circumstances, but become capable of originating painful sensations when diseased or injured.

The work of Lennander, Ramström, and others has proved that this conception is erroneous.

Lennander demonstrated that all painful sensations set up in the pelvic viscera can be assumed to arise in areas innervated by the lumbosacral and intercostal nerves, especially in the parietal layer of the peritoneum. For instance, increased peristalsis set up by an inflammatory condition of the gut acts as a mechanical stimulus, exerting traction on the peritoneum. According to Ramström, traction alone is an effective stimulus for the parietal peritoneum. Lennander believes that all organs innervated by the sympathetic or by the vagus below the origin of the recurrent laryngeal are insensitive; he has found that pain is not excited by stimulation of the anterior wall of the vagina, the uterus, ovaries, and Fallopian tubes.

Next, as to referred pain. The fact that the pain associated with visceral disease is often localised in a cutaneous area rather than in the affected region, was noted many years ago by Lange. Henry Head was, however, the first to investi-

gate the subject systematically and render the results of careful observation and experiment available in practice.

It appears from Head's researches that certain stimuli applied to the viscera are capable of eliciting pain, but pain not localised in the viscera but referred to some cutaneous surface.

The area of reference was constant and, apart from actual pain, was often hyperæsthetic. The constancy of these painful and hyperæsthetic zones render them of much value for diagnostic purposes. Physiologically, the results can be best *described* in terms of the following hypothesis: It may be laid down as a fact of experiment and general observation that if a painful stimulus be applied to, *e.g.*, a point of a normal foot, the resulting sensation is localised near to the point of stimulation; if, however, the sensibility of the skin is impaired in that region, the sensation will be localised in the nearest (physiologically speaking) unaffected point. That is to say, if two spots, A and B, are physiologically associated, for instance, by nervous inter-connections, and if A be an area of lower sensibility than B—it may be normally, or pathologically, owing to disease of the afferent paths—then a stimulus applied to A is localised in B. A viscus is the A of our illustration, and B some corresponding or connected skin area. Following the train of ideas a little further, if A send up afferent impulses to some common "centre" C, an alteration of the state of equilibrium in C may result, with the consequence that if stimuli be now applied to B, an abnormal conscious response may be obtained owing to the modification of the recipient "centre."

The nature of the connecting link between our A and B has also been studied. It was first suggested that posterior root ganglia receiving fibres from viscus and corresponding skin area formed the link. Subsequent work suggested that the correlated parts could be grouped more satisfactorily by a schema derived from our knowledge of the primitive segmentation of the cord.

Recent work has, on the whole, rather tended to support the original hypothesis, but the matter is not yet definitely settled

I have now described some of the main facts known as to cutaneous pain. In the next chapter we shall consider some important modifications of our beliefs due to recent studies.

BOOKS, ETC., RECOMMENDED FOR FURTHER STUDY

PAIN—

Thunberg, op. cit.

Psycho-physiologie de la Douleur, par *I. Ioteyko et M. Stefanowska*, Paris, Alcan, 1909, pp. 249. (Contains a fairly good bibliography. Must be read critically.)

Richet. Art. Douleur, Dict. de Physiologie. (The same remarks apply as in the previous case.)

REFERRED PAIN, ETC.—

Consult the numerous papers by Head and his collaborators which have appeared in Brain from 1888 onwards.

CHAPTER IV

PROTOPATHIC AND EPICRITIC SENSIBILITY

THE reader who has examined the results epitomised in the last two chapters will have noticed that, mainly in consequence of the researches initiated or inspired by Max v. Frey, a fairly coherent description of the sensory mechanisms of the skin has been reached. In effect, it has become customary to regard the cutaneous surface as a vast congeries of points each responding to stimuli by a specific afferent impulse, the heat spots responding by a sensation of heat, the touch spots by one of touch, and so on. The whole conception is conveniently resumed by the phrase "Punctate Sensibility."

Although this belief certainly reflects the opinions of a distinct majority of workers, and adequately presumes a large number of careful observations, objectors and difficulties have not been wanting. Oppenheimer, for instance, has sharply criticised v. Frey's interpretations of his experiments, and the state of sensation after injury to nerves or section of them has been difficult to reconcile with the doctrine of punctate sensibility.

It was plain that a careful study of the sensory changes associated with division of cutaneous nerves must throw needed light on the nature of the mechanisms concerned. It was equally apparent that the necessary conditions of such study would never be fulfilled by the casual subjects of accidental injury, since the training and experience necessary for really efficient work on cutaneous sensibility are, perhaps, greater than for any other branch of sensory research. Dr. Henry Head of the London Hospital was the first man of science to realise practically the importance of these considerations. To the enthusiasm and ability of this worker,

together with his collaborators, Rivers, Sherren, Ham, and Thompson, we owe the initiation of a new epoch in sense-physiology. Other workers have not been slow to avail themselves of Head's pioneer work, *e.g.* Trotter and Davies, who have recently published an interesting contribution to the subject.

Signs are not wanting that the method of direct experiment upon man, naturally under conditions which preclude as far as humanly possible the risk of permanent injury, will enable us to complete and co-ordinate the results of ordinary experimental physiology.

When one remembers the essential difficulty of psycho-physiological work, it is not surprising to find that the results of the pioneer researches are not in all respects concordant. It is also probable that subsequent progress will necessitate essential modifications in the theoretical schemata proposed by the observers. I shall describe those portions of the work which seem to be best established, and finally indicate the theory of the matter which seems at the moment to be the most adequate working hypothesis. It is to be remarked that any one really interested in the matter should examine the original papers.

When the median nerve is divided, sensation is entirely lost over a considerable part of both index and middle fingers; over the palm, within the area said by anatomists to be supplied by this nerve, sensation is usually diminished but not completely lost. Similarly, division of the ulnar produces complete anæsthesia of the little finger and of a variable portion of the ulnar aspect of the palm. Partial loss of sensation occurs over a larger aspect of the palm and of the ulnar surface of the ring finger.

On examining what is meant by saying that sensibility is diminished in a part of the ulnar territory, we find that what really happens is that certain sensations are completely lost and others retained. If in a patient who has divided his ulnar nerve the ulnar half of the palm be stimulated with cotton wool no sensation will be produced, while the lightest touch will be appreciated directly the line corresponding to the axis of the index finger is passed. Compass points 2

centimetres apart are not distinguished, nor temperatures between 22° and 40° Centigrade.

"When the hand has settled down after the shock of the injury that has divided one or more nerves to the palm, it will be found that although the area we have spoken of is totally insensitive to certain higher forms of stimulation, a stimulus producing pain over normal parts, *e.g.* a prick of a pin, causes a more unpleasant effect than over normal parts. If the nerve has been united, sensation begins to return after a variable interval. The first sign of recovery is a gradual diminution in the extent of the area insensitive to pain and to all forms of heat and cold."

Eventually no part remains irresponsive to all stimuli, and at a time when the boundary of light touch is still distinct, responsiveness to pin prick and thermal stimuli has much improved.

At this stage, painful stimuli produce effects which radiate widely and are particularly unpleasant. Ice and water at 50° C. can be detected as cold and hot, but no intermediate degrees.

These observations were made on hospital patients. We now come to the experiment on Head himself.

The radial and external cutaneous nerves were divided near the elbow with aseptic precautions, and the ends sutured together. Immediate examination of the surface innervated by the divided nerves showed the following condition:—

(*a*) Very moderate pressure was appreciated and well localised, but touches with cotton wool or deformations of the skin produced by drawing hairs *outwards* were without effect.

(*b*) Compass points even 8 centimetres apart could not be distinguished.

(*c*) Heat, pain, and cold were all lost.

(*d*) Between the margin of the analgesic area and that insensitive to cotton wool lay a zone where the prick of the pin was abnormally painful.

(*e*) None of the cold spots marked out before the operation reacted to ordinary stimuli.

It will be seen that the responsiveness still existing within the analgesic area was merely to forms of stimuli which pro-

duced inward deformation of the skin, and may be supposed to have acted on the end organs below the cutaneous level; that is to say, there was, as we should expect, a conservation of deep sensibility. The importance of the observation is, that it illustrates that much which is attributed to cutaneous sense organs is really due to a quite different afferent system. Trotter and Davies, who have made somewhat similar observations, desire to restrict the term "Sense of Pressure" to the afferent correlate of deforming stimuli and to keep the word touch for strictly cutaneous sensibility. Although a distinction of this kind is desirable for the sake of a clear terminology, I am not certain that the separation of the effects by an introspective analysis is so definite as these authors hold.

Within the analgesic zone, no change was observed for seven weeks; at the end of that time sensibility to pin prick returned, and was complete in about 200 days. At this stage it was found that ice and water at 50° C. could be sensed as respectively cold and hot, but no "intermediate" sensations of warmth or coolness were detected. The areas from which these sensations were obtained coincided with the hot and cold spots. The cold spots reacted to stimuli from 0° to 24°, the hot ones to temperatures from 38° to 45°. A curious observation is the following: A cold spot of unusual activity was stimulated by means of a copper cylinder 1 mm. in diameter cooled to the temperature of melting ice. This produced a sensation of cold. Water at 20° C. was then placed in a test tube with a flat bottom of 1 cm. diameter applied to the skin in such a way that it stimulated a constellation of spots, including the one originally stimulated. The resultant sensation of cold was more vivid than that produced by stimulating a single spot with a considerably lower temperature.

Pain, as recognised at this period, exhibited marked peculiarities. No exact punctate distribution could be ascertained. The minimal stimulus requisite to produce a response was higher than for normal parts, but the response when produced was peculiarly unpleasant, radiating and tending to be localised in remote parts.

These phenomena of radiation and remote reference were specially characteristic of this stage of recovery. Deep sensations—in the sense used above—were well localised, but as recovery proceeded this power was lost or obscured.

"To evade the localisation due to deep sensibility we employed minute drops of ether or of ethyl chloride, instead of the ice-cold tube; the characteristic radiating and referred sensations of cold then appeared unhampered by the consequences of pressure. Such a stimulus applied to the wrist might cause the whole affected area on the back of the hand, including the greater part of the thumb, to become icy cold, and stimulation of a group of spots on the forearm was followed by an intense coldness over the whole dorsal surface of the thumb."

We have, therefore, at this stage a fairly well defined group of sensations, viz. sensibility to temperature stimuli restricted to two categories, the hot and the cold, and elicited by stimuli of widely different intensities; sensibility to pain, abnormally difficult to bring over the infra-conscious threshold associated with marked "Unlust," radiating and often referred.

This kind of sensibility is termed by Head PROTOPATHIC.

After a variable time the skin again becomes sensitive to light touch and moderate grades of temperature stimulation. Compass points are discriminated, and the radiation characteristic of the former stage disappears. These later-returning sensibilities are called EPICRITIC.

It is evident that the desirability of forming these two classes will depend on whether we can answer the following questions in the affirmative:—

(1) Does any part of the body normally exhibit a responsiveness of the protopathic type only?

(2) Can protopathic and epicritic areas be delimited with accuracy either (a) *in point of time* or (b) *spatially* within the region deprived of cutaneous afferent paths by *experimental* division of nerves?

Head and Rivers have, in my opinion, made out a very strong case in favour of their conclusion, that the glans penis is endowed with protopathic and deep sensibility alone.

"The glans is entirely insensitive to stimulation with

cotton wool and with the tactile hairs. . . . As soon as hairs of greater bending-strain, the so-called 'pain-hairs,' are used, the glans is found to be sensitive to from 70 to 90 grm./mm^2. This produces a characteristic diffuse boring or stinging pain much more unpleasant than over the skin of the penis or foreskin; v. Frey specially remarks that the pain is of a different character from that over the normal skin."

Although no sensations of heat seemed attainable, perhaps owing to the absence of heat spots, water from 0° to 21° C. produced an intense sensation of cold. In the other subject heat spots were present round the meatus, and water above 40° was always called warm. No response was obtained with temperatures between 26° and 37° C. It is obvious that these results agree well with the characters of protopathic sensibility as above described.

Although much interesting evidence is adduced, it is not clear that the answer to our second question is quite so decisive.

A small triangular area on Head's wrist is described in the following terms:—

Deep sensibility was undoubtedly present. There was also definite responsiveness to cutaneous stimulation, either in the form of moderately fine v. Frey hairs or cotton wool, and the point of application of such stimuli was well localised. Cutaneous pain was entirely absent. "Strong interrupted currents unbearably painful over the normal skin produced the characteristic whirring sensation devoid of any element of pain. The observations on thermal sensibility within this area are not quite so definite. It seems to be clear that at first no stimuli below 22° produced a response, that is, at a time when touch was accurately localised. In the same way no heat spots were present, but temperature stimuli acting upon comparatively large surfaces (diameters of 1 or more centimetres) were said to call up a sensation of warmth if between 42° and 48°. Tubes at 50° or higher temperatures elicited a sensation of contact, but no thermal response." Head and Rivers observe that one of their chief experimental difficulties was "the tendency which Head showed to call cold stimuli 'warm' within the limits of

the triangle. Whenever a thermal sensation was produced at all, it was one of warmth; some of the most satisfactory warm sensations were evoked by an ice-cold tube, and yet, at this time, temperatures of 50° C. and above were not appreciated."

Eventually responsiveness to painful stimuli was restored and a thermal sensibility of the ordinary punctate form.

In describing the state of affairs within the "triangle" I have availed myself of the complete account published in Head and Rivers' latest (November 1908) memoir. This paper was not, I think, published when Trotter and Davies wrote their criticism of the work. Some of their remarks, therefore, are at best applicable to the statement of the case as described in the preliminary communication of Head, Rivers, and Sherren. In view of the fact that stimuli between 42° and 48° called up a sensation of warmth, together with the other phenomena noted, I am of opinion that the suggestion of Trotter and Davies that the thermal sensibility was hallucinatory, or—as generally termed—paradox warmth, occurring within an area of ordinary thermo-anæsthesia, cannot be accepted. Indeed, although as a pure theorist I feel it to be presumptuous to criticise the opinions advanced by such careful and experienced observers as Trotter and Davies, their views on the mechanism of thermal sensibility are not, I think, entirely consistent. Thus they write (*op. cit.*, p. 147): "Of two grades of the sensation of warmth it cannot be said that there is anything in the one which is not in the other, the difference is one purely of intensity; on the other hand, between the sensation of heat and the most marked warmth there is a distinct difference of quality—heat possesses a certain abruptness and, so to say, brightness which warmth lacks."

On the following page of their memoir, however, I find this passage (*op. cit.*, p. 148): "When a temperature spot has its sensitiveness reduced, the sensations roused by the appropriate temperatures are reduced in intensity, so that, for example, on a heat spot a temperature which gave before a sensation of warmth now gives indifferent warmth or indifference, while on a cold spot a temperature which gave

cool now gives indifferent cool or indifference. The same of course applies to the maximal sensation in each case—warmth is felt instead of heat, cool instead of cold." On the whole, the reader will perhaps conclude that Head and Rivers have established a *prima facie* case in support of the view that, the second fundamental question must be answered in the affirmative, so far as temporal separation is concerned.

As to whether this is also true for the second part of the question seems much more doubtful. It does not appear in view of Trotter and Davies' work, that in the partly anæsthetic areas due to nerve section a sharp border between regions of protopathic plus deep sensibility and deep sensibility alone can be made out. The question, however, turns so largely on the respective values of the techniques used by Head and Rivers on the one hand and Trotter and Davies on the other, that I do not think those who have not actually experimented themselves can usefully formulate opinions.

Head and Rivers express their general conclusions in the following way:—

(1) The skin is supplied by two anatomical distinct systems, the epicritic and the protopathic, which regenerate at different periods after section of an afferent nerve, and may be one or other, alone present in certain regions. The glans penis is an example of a part supplied by the protopathic system only, while the triangular area on Head's arm was, for some time, innervated through the epicritic system alone.

(2) Protopathic sensibility depends on the existence of specific end organs, the areas between such organs being, in the absence of epicritic innervation, insensitive to purely cutaneous stimulation.

(3) In a part supplied by protopathic end organs alone any sensation evoked radiates widely and tends to be referred to distant parts. Radiation and reference are abolished when the part becomes sensitive to cutaneous tactile stimuli and intermediate thermal stimuli.

(4) Thermal adaptation is a function of the epicritic system.

(5) Touch spots are not analogous with heat, cold, or pain spots.

(6) All protopathic organs have a high threshold; the heat spots do not react to temperatures below 37°, nor the cold spots to temperatures above 26°. The pain spots on the back of the head are not sensitive to pressures below 70 grm./mm^2.

Epicritic organs, on the other hand, have a low threshold, responding to temperatures between 26° and 38°, and to tactile stimuli (on the back of the hand) of 12 grm./mm^2.

It will have been noticed that a cardinal distinction between epicritic and protopathic sensibility is the uniformly lower threshold value of the former. It is also to be remarked that when the afferent impulses have reached the spinal cord no separation into epicritic and protopathic groups can be made out. In certain forms of hæmorrhage into the cord, motion is lost in one limb and all forms of sensation in the other. The careful researches of Theodore Thompson seem to have established the following conclusions with respect to intra-spinal conduction:—

The ascending paths are three in number, one carrying up painful and thermal impulses of *all* forms, a second conveying tactile impulses, and a third those connected with the sense of position. The distinction between protopathic and epicritic systems is therefore definitely sub-spinal.

We may perhaps sum up the discoveries of Head and Rivers with the help of the following theoretical schema:—

In the peripheral nerves there exist two conducting mechanisms functionally and, it may be, anatomically separate. One system is relatively impermeable to incoming impulses, and represents a more primitive type of nervous organisation; the other, more delicately organised, less resistant to impulses, representing a more complex type of nervous system. This second system, in virtue of its more delicate organisation, will be regenerated after nerve injury in most cases more slowly; it will fail to transmit the results of strong stimuli, being as it were temporarily disorganised by them, and will be less widely distributed than the former system. The first, or, to use a rude electrical analogy, high

tension system is Head and Rivers' protopathic system, the second, or low tension, their epicritic system. The sole or main difference between the two classes is one of finer or coarser organisation in the afferent paths up to the cord. In the cord itself, resistance to all forms of impulse becomes the same.

These brilliant discoveries enable us to form some rational conception of the manner in which, through the conflict of sensory impulses, peripheral specialisation has come about. At one time we may suppose high threshold stimuli alone produced a response; fine sensory discrimination was not an important factor in the struggle for existence owing to the imperfect adaptation of the whole organism to its environment. At this stage all sensibility was protopathic. As adjustment became less imperfect, selection for finer powers of sensory discrimination began to operate, and we reach the germs of an epicritic system.

This train of thought can be applied to the process of natural selection, not merely between organisms taken as a whole, but between different parts of the same organism, the inter-cellular struggle for existence, to which Le Dantec has called attention.

Certain parts of the superficies are from their situation, and the necessity for their performance of specialised functions, not likely to have to deal with the finer processes of sensory discrimination. An admirable illustration is afforded by the external genitalia. It is clear enough that coitus does not require a sensory mechanism of the specialised grade associated with the epicritic system, and we have seen that the glans penis is furnished with protopathic and deep sensibility alone.

A further extension of the ideas sketched in the preceding paragraphs may be left to the reader, who will, I think, speedily realise how fruitful and important in many directions are the researches discussed in this chapter.

PAPERS RECOMMENDED FOR FURTHER STUDY

Head, *Rivers*, and *Sherren*, The Afferent Nervous System from a New Aspect, Brain, 1905, xxviii. 99.

Head and *Thompson*, The Grouping of Afferent Impulses within the Spinal Cord, Brain, 1906, xxix. 538.

Head and *Rivers*, A Human Experiment in Nerve Division, Brain, 1908, xxxi. 324.

Trotter and *Davies*, Experimental Studies in the Innervation of the Skin, Journal of Physiology, 1909, xxxviii. 134.

Thompson, On Certain Changes in Sensation which Occur in Cases of Cross Lesions within the Spinal Cord. M.D. Thesis, London, 1906. Jarrold and Sons.

CHAPTER V

TASTE AND SMELL

THE senses of taste and smell have many points of resemblance, one being the scantness of our knowledge respecting the physiology of either.

The researches of the Greeks respecting the psycho-physiology of taste have not been fruitful, although in the *Timæus*, Plato uses language which can be understood to imply that the physical basis of gustatory stimulation is chemical.

At present we must confess ignorance as to the real mechanism of the stimulation processes, and admit that the end organs themselves, and the paths by which impulses arising in the end organs are transmitted to the brain, have not been determined with great exactitude.

The ostensible end organs, the taste buds comprising "gustatory" and supporting cells, are somewhat widely distributed. They occur on the upper surface of the tongue, the soft palate, the posterior surface of the epiglottis, and, to some extent, within the larynx.

Whether the gustatory cells are really end organs in the sense in which this term may be applied to the retinal cones and rods, or whether they merely act as props upon which the nerve endings twine, is a matter of doubt.

Within the sensory province of taste we can recognise but four sensation-qualities—the sweet, the salt, the acid, and the bitter.

Investigation can be made with the help of several methods. The simplest, that used by Oehrwall and many others, is to apply a fine camel's-hair brush dipped in test solutions to individual papillæ, the latter being illuminated by light reflected from a small concave mirror.

Toulouse and Vaschide employ a large number of test solutions of different strengths; a measured volume, the same in each experiment, is placed in the subject's mouth, and he must immediately state what he feels. Numerous blank experiments—the same volume of distilled water—are interpolated, and care is taken that all the solutions shall be at body temperature, a very important point.

Sternberg has introduced an ingenious method by the aid of which stimuli can be minutely localised. This observer finds that the vapour of ether when blown upon the tongue produces a sensation of extreme bitterness, and that, in a similar way, chloroform vapour is very sweet. A glance at the diagram of his instrument (Fig. 1) will give the reader an idea as to its practical use.

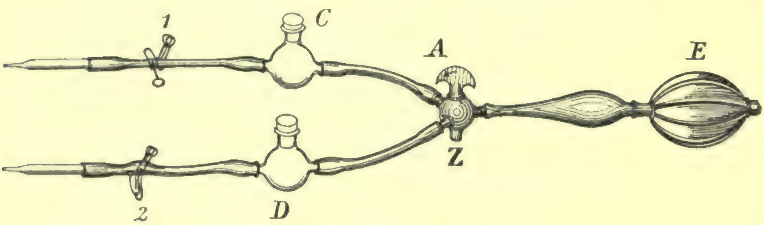


FIG. 1.—*A* and *Z* rubber tubes leading from two-way tap to glass-bulbs *C* and *D*, which contain Ether and Chloroform respectively. By means of the rubber-bulb *E* a stream of air can be directed along *E*, *A*, *C*, 1, or *E*, *Z*, *D*, 2, at will.

Of the three methods, that of Toulouse and Vaschide is probably the most convenient for clinical work, and that of Sternberg for localising experiments.

It is quite clear that the tongue, which is the organ of taste, at least in a popular sense, is not equally sensitive in its various parts for all forms of stimuli.

According to popular belief, bitter substances are best tasted with the back of the tongue, and sweet ones with the tip. Schreiber found that responsiveness to bitter stimuli was restricted to the back and extreme borders of the tongue; the insensitive areas for salt and sweet comprise the antero-medial portion of the dorsum linguæ; while the whole upper

surface responds to acid except a very small portion rather nearer the tip than the root. Within this latter region, of course, no sensation can be elicited.

The actual measurements of the insensitive area are variable, and it does not seem to exist in children.

With regard to the individual papillæ, Oehrwall's original work has not been superseded. He asserted that the filiform papillæ are quite insensitive. Oehrwall tested 125 papillæ (filiform, fungiform, and circumvallate); 27 did not react to acid, bitter, or sweet; 60 reacted to all three; of the other 28, some reacted to acid and sweet but not to bitter, others to one form of stimulus only. The fact that Oehrwall found that an electrode applied to, *e.g.*, an acid-reacting papilla called up a sensation of acid cannot be considered to prove Müller's law for this sensory field. There is reason to think that electrolytic decomposition of the saliva is responsible for the result obtained.

There is no good evidence that sensations of taste can be excited by mechanical stimulation (v. Kiesow) of the tongue.

In connection with taste, phenomena analogous to visual contrast, both simultaneous and successive, have been observed. After tasting weak sulphuric acid distilled water seems sweetish, and a 0·1 per cent. solution of sodium chloride increases the stimulus value of a weak glucose solution.

Simultaneous application of sugar and salt to opposite borders of the tongue increases the effectiveness of both stimuli. Some drugs affect particular sensations, a well-known example being the case of *Gymnema sylvestre.* If the leaves of this plant be chewed, or if a sodium salt of gymnecic acid be painted on the tongue, a very strong solution of sugar does not taste sweet nor quinine bitter. Salt and acid stimulation are not however affected. These effects, which pass off in a few minutes, are very striking.

Considerable attention has been paid to determining whether chemical affinities exist between substances which elicit the same sensation of taste. Wilhelm Stirnberg has been especially active in this direction, but it cannot be said that any very definite results have been obtained.

The path by which gustatory impulses reach the brain

has also been much studied, and the results are curiously conflicting.

Taking the front of the tongue, it is certain that the impulses first run in the lingual nerve and then in the chorda tympani. Thus Lussana divided the lingual on one side after its junction with the chorda and on the other side above the junction. In the latter case, taste was unaffected. Many cases of division of the chorda, or middle ear disease affecting it, have been published, in which taste was abolished over the front of the tongue.

The effect of stimulating the central end of the chorda tympani has already been described (Chapter I.).

As we get higher up, our difficulties increase. Some hold that the impulses travel by the pars intermedia of the seventh nerve, others that they re-enter the fifth by way of the Geniculate ganglion, great superficial petrosal, and Vidian nerve.

The evidence on both sides seems to be definite, but is really not so. For example, the fact that complete extirpation of the Gasserian ganglion, in the Hartley-Krause operation for trigeminal neuralgia, has been unaccompanied by loss of taste, would seem to settle the question. But Vaschide has pointed out that what is removed in this operation is not always the Gasserian ganglion. He cites an amusing illustration.[1] An eminent French surgeon exhibited at the meeting of a learned society the Gasserian ganglion excised by him for trigeminal neuralgia. He was ill-advised enough to allow a pathologist who was present to cut sections of the "ganglion," which was found to contain neither nerve cells nor fibres.

I do not therefore think it necessary to insert the various "proofs."

The course of the impulses from the back of the tongue is also uncertain. That they first travel in the glosso-pharyngeal is hardly doubtful, but it is possible that they then reach the fifth by way of Jacobson's nerve and the small superficial petrosal.

The balance of opinion seems, however, to incline in favour

[1] Vaschide, art. "Goût," Richet's *Dict. de Physiol.*, vol. vii. p. 617.

of the glossopharyngeal, of which nerve that of Jacobson is, developmentally, a branch.

It should be mentioned that some fibres from the superior laryngeal branch of the vagus are distributed over the root of the tongue. Their relation to taste is unknown.

We have no knowledge as to the cortical representation of taste, hardly even a conjecture worth repeating. There is a tendency to pick out the anterior sylvian convolution as the cortical "centre," but the evidence is trifling.

The relation of taste to smell will be discussed when we have examined the latter sense.

Smell

Although both Aristotle and Plato were the authors of ingenious speculations on the physical basis of smell, it cannot be affirmed that their work has had much influence on the progress of physiological knowledge respecting this sense. In general terms, it may be said that while the number of exact observations on smell which have now been accumulated is great, their interpretation is obscure.

The area of nasal mucosa associated with the perceptive mechanism of the sense is smaller than used to be thought, comprising a rectangular strip situated over the upper part of the superior turbinated bone, together with a corresponding patch upon the septum.

That the "olfactory cells" of the histologist are the end organs is hardly doubtful, since the proximal extremities are non-modullated nerve fibres of the first cranial (olfactory) pair.

Three methods of examination may be described.

Zwaardemaker's Olfactometer

This consists of two concentric cylinders, the inner terminating in a nose piece. The outer cylinder is lined with some odorous substance, *e.g.* indiarubber or "hoof cement." When the inner cylinder is pushed in level with the outer

one, air inhaled through the instrument does not pass over the layer of indiarubber.

The further the inner cylinder is drawn out, the greater the surface of indiarubber exposed to the in-drawn air.

FIG. 2.

The extent to which it is necessary to withdraw the inner cylinder before the odorous substance can be recognised is a measure of responsiveness to that particular stimulus.

Method of Toulouse and Vaschide

A series of solutions containing camphor is prepared. The solutions vary in strength from 1 in 1000 to 1 in 1,000,000. These are placed in flasks, each holding 10–15 c.c., and having an opening of 17 mm. diameter. A similar flask containing distilled water serves as a control.

Grazzi's Method

A square of blotting-paper, 5 cm^2., is moistened with 10 drops of 20 per cent. benzoic acid in alcoholic solution. The alcohol is allowed to evaporate, and the blotting-paper is preserved. A series of cards are made which exactly cover the square of blotting-paper, and in the centre of each a hole is made. The diameter of the aperture varies from 0·5 to 5 cm. A card is placed over the blotting-paper, and a little hollow cylinder, 30 by 5 cm., is applied to the card, including the hole. If the patient cannot detect the odour of benzoic acid, another card is used with a larger hole in it, until the threshold is reached.

Of these different plans, that of Zwaardemaker has yielded the best laboratory results, while the method of Toulouse and Vaschide is more convenient for the testing roughly of a large number of people. Grazzi's method is

not, so far as I know, largely used, and I cannot give any details as to its practical applicability. The routine investigation of the olfactory sense demands a certain amount of patience and care on the part of the operator. The methods generally adopted in the wards of hospitals by clinical clerks and others are unlikely to yield any results of value. The same remarks apply to the investigation of taste.

It would seem probable that in order to stimulate the olfactory end organs, substances must be either gaseous or sufficiently finely divided to be suspended in a gaseous medium.

It is generally held that liquids are odourless. This was first rendered probable by Weber, and more recently by Haycraft.

"The person to be experimented on lies upon his back on a bench with his head hanging downwards over the end so that the olfactory region of the nose is lowest. Two glass funnels are connected by tubing with a T junction, and from the third limb of the T another tube passes into one nostril; warm normal saline is allowed to flow from one funnel until both nasal cavities are filled, and the air-free solution falls upon the ground. This is then displaced by warm-scented normal saline."[1] In this way Haycraft could detect no odour in a 5–10 per cent. solution of eau de Cologne.

Experiments of this kind have not escaped criticism.

Aronsohn has objected that strong solutions of substances, such as eau de Cologne, produce inflammation of the nasal mucosa, and that the negative results depend on the latter circumstance. This author has brought forward some evidence to show that moderately strong solutions of odoriferous bodies can be smelled, although it is not certain that in his experiments all air was driven out of the nostrils. It is, however, a fact in favour of Aronsohn's view, that solutions of many salts which do not stimulate the sense of smell under ordinary circumstances appear to do so when the nostrils are filled with a solution.

[1] Haycraft, *Schäfer's Text-book of Physiology*, vol. ii. p. 1256.

There is reason to think that the stimulation of the true olfactory end organs is best effected by moving particles, and that in this way we can distinguish between "common" and real olfactory sensation in the nose.

If one breathes deeply for a few minutes it is possible to hold the breath comfortably for 80 to 120 seconds at least. If a bottle of ammonia is unstoppered under the nose while the breath is held, one experiences a tingling sensation, but no distinct smell of ammonia. If after waiting a minute one pinches the nose to imprison some of the vapour and goes into another room containing no ammonia, at the first inspiration through the nostril the smell of ammonia can be detected.

Although the distinction between olfactory and "common" sensation cannot be made absolute, the general conclusion which may be drawn from this experiment appears to be sound, and is supported by other pieces of evidence. Some amusing experiments can be carried out with snuff. The pungency of snuff is said to depend on the presence of free ammonia and free nicotine, while in the process of manufacture various perfumes or "sauces" are added.

Of the varieties commonly sold, "Princes Mixture," "Morton's Mixture," and "Kendal Brown" are scented, while "Rappee" and Wilson's "S.P." are plain. If a pinch of snuff containing but little perfume be taken, it will be found that the odour of the snuff is only detectable during the actual inspiratory sniff, while the pungent sensation produced in the nose persists when the breath is held, and may even not appear before the "smell" has passed off. It may be remarked that the pungency of the snuffs sold appears to vary with the dryness and state of division. Thus "S.P.," which is dry and finely divided, is extremely pungent, while "Brown Rappee," which is coarse and somewhat moist, is far less so.

The path taken by the inspired air stream through the nostril is of some interest, and has been studied in various ways. E. Paulsen divided the head of a cadaver in the mesial plane and placed squares of red litmus paper over the mucous membrane of the nasal cavity. The two halves were then placed in apposition, and a stream of air saturated with

ammonia vapour was drawn through by a pump attached to the trachea. In this way the path was mapped out by the blue patches of litmus.

As a result of this and similar experiments it would seem that no air is directly drawn over the olfactory mucous membrane, but sweeps round below it. A partial displacement must, however, be produced, and the olfactory "sniff" probably sets up vortices. As Nagel points out, olfactory stimulation through the posterior nares is more important, biologically, to man than that set up by way of the anterior nares.

A classification of the different specific sensations of smell is impracticable, as has been tacitly recognised by mankind at large. In no language do we find a distinctive vocabulary for the objects of this sense. Similarly, the attempt to reduce the various forms of olfactory stimuli to terms of a few components, despite the indefatigable researches of Zwaardemaker, has not led to any very satisfactory conclusions.

In the course of his work Zwaardemaker made many interesting discoveries as to the antagonism between certain odours. Thus iodoform may be antagonised by balsam of Peru, and the odour of musk by that of bitter almonds. Such an antagonism might be physical or chemical, but certain results could hardly be explained in this way. For instance, Zwaardemaker, using a double olfactometer, *i.e.* two instruments of the type already described, performed the following experiment:—

The vapour of a 2 per cent. solution of acetic acid was led into one nostril and that of a 1 per cent. solution of ammonia into the other. If ammonia alone could be detected, the amount of the acetic acid vapour passing to the other nostril was increased, and conversely. Finally a point was reached at which no odour was perceptible at all, although either acting by itself produced a sensation. The following are the chief antagonistic pairs from this point of view:—

Musk and Oil of Bitter Almonds.
Caoutchouc and Paraffin.
Ammonia and Acetic Acid.
Volatile Oils and Iodoform.

This is, perhaps, the only well authenticated example of two stimuli, each separately effective, when simultaneously applied failing to produce a response with which we are acquainted in sense physiology.

As would be expected, many of the analogies to contrast and fatigue already noticed in the case of gustatory stimulation can be made out for smell. Thus after smelling cumarin, a mixture of cumarin and vanilla only smells of vanilla. After stimulation with tincture of iodine, alcohol and copaiba balsam appear odourless; some ethereal oils are weakened, others not affected. Prolonged stimulation with ammonium sulphide removes the responsiveness to sulphuretted hydrogen and bromine, but not to ethereal oils.

Normally, the delicacy of the sense of smell is variable. Toulouse and Vaschide distinguish between the general and specific threshold values for smell. The general threshold value is the strength of solution which the subject recognises not to be distilled water, but cannot tell exactly what it is. The specific threshold value is the strength of the solution which can be detected and recognised as a specific body.

Some of their main results were as follows (the fraction represents the strength of the camphor solution used) :—

	General Threshold.	Specific Threshold.
33 males . . .	9/100,000	4/10,000 (mean values).
37 females . .	1/100,000	5/10,000 ,,

Vaschide and Toulouse also tested 163 children from Villejuif, dividing them into three groups: 3–5 years, 6 years, 12 years. The general threshold diminished steadily to the age of 6 years and then increased. The specific threshold diminished steadily. Ten dilutions, from 1/1,000,000 to 1/100,000, were submitted to ten children in series. All the children recognised 5/1,000,000.

The possible sources of fallacy in work of this kind are many, so that it is not surprising that different observers obtain contradictory results, especially as they have not employed any adequate statistical method of reducing their observations.

There is no satisfactory evidence of any sexual difference

in olfactory acuteness. There is some reason to think that smokers are less sensitive than non-smokers. It is not true that the blind have an abnormally acute sense of smell (Griesbach).

Minor abnormalities in the sense are common, and may be due to disease—*e.g.* catarrh—or are congenital. Cloquet reported the case of a person unable to smell vanilla; Nagel refers to an English chemist who could not detect any odour in hydrocyanic acid; while many persons, it is said, cannot smell mignonette. Temporary anosmia (loss of smell) can be induced by the local application of cocaine or morphia. On the other hand, hyper-sensitivity, or hyperosmia, is not rare in certain neurotic conditions, and can be induced by the administration of certain drugs, of which strychnine is the best known.

The inter-relationships of taste and smell are numerous, and most of what is generally called taste must be referred to olfactory stimulation. This needs no proof to any one who has suffered from a cold in the head. It is not so generally known that stimuli which only operate on one of the two mechanisms may be antagonistic. Thus tinct. aurantii, which has no real "taste," neutralises the bitter taste of quinine, and effervescing drinks diminish the nauseous flavour (olfactory stimulation) of castor oil.

The path of impulses to the brain would seem to be involved in no uncertainty, but there is a little evidence that olfactory impulses *may* reach the brain by channels other than the olfactory nerves.

Magendie destroyed the olfactory nerves in a dog right down to the lamina cribrosa. The animal recovered from the operation, and Magendie presented it with several paper parcels of the same size, some containing cheese and others wood. The dog selected and unwrapped the packets of cheese without hesitation.

Claude Bernard performed an autopsy on a woman of twenty-nine in whom the olfactory bulbs were absent and the lamina cribrosa imperforate. He traced out her friends, and found that her sense of smell had been perfectly normal. She had complained of people having smoked in her room and of a

neighbouring sewer. She had also been fond of smelling flowers. Somewhat similar cases have been reported by Lebec and Heschl. While it is foolish and unscientific to distrust evidence merely because it is old, we should bear in mind that these cases were published a good many years ago, and that, at the least, such a condition as they reveal is excessively rare.

Finally, a few words must be devoted to the psychology of smell. The relation of smell to memory is, as Professor James remarks, one of the favourite topics of popular psychology. Oliver Wendell Holmes happily summarised one's ordinary experience in the following words: "Memory, imagination, old sentiments and associations are more readily reached through the sense of smell than by almost any other channel." Technically, this amounts to saying that smell is an affective sense; *i.e.* stimulation of its mechanism results rather in a general alteration of feeling-tone of the general atmosphere, as it were, of consciousness than in any distinctly localised or delimited impression. An illustration of this is that we do not project our olfactory sensations to any great extent, if at all. In consequence, olfactory impressions tend to be associated with a sum-total of feeling-tone and with other impressions which also affect the conscious atmosphere as a whole. It is accordingly easy to understand why, in many animals and some men, olfactory stimulation is associated with sexual excitement.

Bunge, among others, has urged that the sense of smell is protective in character, and points out that noxious gases, *e.g.* sulphuretted hydrogen, are malodorous. The objections to this are of comparatively little weight, in my opinion. It is perfectly true that some highly poisonous gases, such as carbon monoxide, have no smell, but it seems to me that few or none of them are of frequent occurrence in a state of nature. It is a tempting speculation—but no more than a speculation—that all gases originally excited the end organs of smell; that natural selection favoured those animals whose end organs reacted most strongly to toxic gases; and that panmixia eliminated gradually responsiveness to normal atmospheric constituents, or that responsive-

ness to the latter was correlated with some harmful variation.

The cortical representation of smell is doubtful; some results suggest the hippocampal region, but the connections of the olfactory tract are numerous and complicated, while experimental work on lower animals is beset with serious difficulties.

The delicacy of the receptive mechanism in such animals as the dog must be exquisite, since the blunted sense of man can detect some substances (*e.g.* mercaptan) in a dilution of one in fifty thousand millions!

WORKS RECOMMENDED FOR FURTHER STUDY

TASTE—

L. Marchand, Le Goût, Paris (Biblio. de Psychol. Expér.), 1903, pp. 328. A full account with literature to date of publication.

W. Nagel, art. Geschmackssinn, Nagel's Handb., Bd. iii. p. 621. A very readable sketch.

N. Vaschide, art. Goût, Richet's Dict. de Phys., vol. vii. p. 571. The most complete account in existence. A very full and fairly critical bibliography.

W. Sternberg, Geschmack und Geruch, Berlin (Springer), 1906, p. 149. Contains some interesting remarks on technique.

SMELL—

H. Zwaardemaker, Physiologie des Geruchs, Leipzig, 1895. The standard treatise.

H. Zwaardemaker, art. Geschmack, Ergebnisse d. Phys. Jahrb., 1903, 2nd Abth., pp. 699, etc.

W. Nagel, art. Gerchssinn, Handb. d. Phys., vol. iii. p. 589. Thoroughly good.

(The best accounts in the English language are by Professor J. B. Haycraft in the second volume of Schäfer's Text-book of Physiology.)

CHAPTER VI

THE SENSE OF POSITION AND MOVEMENT

In the next two chapters I shall discuss a division of our subject which is difficult to arrange in orderly fashion, but of extreme interest.

The ordinary experience of life teaches us that in health we possess the faculty of poising our bodies in space with great precision; we are also capable of adjusting the several parts, in particular the limbs, to the performance of duties requiring a minute accuracy of localisation.

These powers of general and local equilibration show themselves to a marked extent at a very early period of life; indeed great as are the effects of special training and experience, late acquirements are small in comparison with the powers developed as a normal event in the process of growth. The difference between the most skilful of dancers and the ordinary child of six is not so vast as that separating the normal child and one of the same age who, either through disease or accident, cannot walk.

Extending our survey to other members of the animal kingdom, we see in all but the most primitive phylla equally remarkable powers of equilibration. The problem is to determine what mechanism or mechanisms are essential for the performance of these functions.

It is at once obvious that we can make an elementary distinction between the efferent and afferent processes involved. Evidently both general and local equilibration demand an efficient muscular system and an efficient efferent nervous system through which impulses can reach the muscles or corresponding executive organs. This side of the problem does not require any discussion. When we turn to the afferent and receptive side of the matter, however, difficulties begin to accumulate. In the first place, is it necessary to

suppose that there are any special paths or receptive structures dedicated to the sense of equilibration, whether local or general, or can we account for the facts by way of the actual or stored (memorised) impressions which result from the stimulation of other sense organs, those of touch, smell, hearing, and vision? Now it is quite probable that many facts akin to those just mentioned can be accounted for quite simply. An example is the sense of direction in pigeons, and—although this is less clear—the homing flight of bees can perhaps be regarded as another illustration. Exner's observations on pigeons are so interesting that I shall describe them. Pigeons were placed in a basket covered with a black cloth, and the basket was shaken or made to turn on its axis during the whole outward journey. They were released 37·7 kilometres from Vienna, separated from that city by mountains and in a spot which their owner believed they had never before visited. A second batch were treated in the same way, except that the basket containing them was not rotated. The pigeons were released one after the other, not one before its predecessor has disappeared. All reached home safely. In a second experiment galvanism was tried. Four pigeons were used, two old and two young ones, one old and one young pigeon being galvanised and rotated; the distance was 54 kilometres. The old galvanised pigeon reached home in 3 hours 32 minutes, the old normal pigeon two days later. Neither of the young pigeons got home. These experiments evidently suggest that visual impressions are, as Forel holds, adequate to account for the facts. Exner also tried to find out whether the pigeons acquire any information on their outward journey. He anæsthetised two pigeons during the whole of a journey of 43 kilometres, and then left them four days at Oberhollabrun separated by hills from Vienna; they were then released together with a control pigeon. Of the three, one of the anæsthetised pigeons reached home in 4 hours 20 minutes, the other two birds being lost. In another experiment, over a less distance, two old and two young birds were used, one of each age being anæsthetised. Both the old birds got home, the anæsthetised one first; the young ones were lost.

Forel in describing these experiments remarks: "I am astonished that Exner does not draw from such clear results the simple conclusion that it is the experience and the knowledge of places by vision that orients pigeons."[1]

The quotation illustrates the somewhat trenchant fashion in which Forel settles rather complicated matters, but it does appear that the results are consistent with his view, although, as we shall see later, that is good reason for thinking that the pigeon has quite special equilibrating organs. It may be remarked that the term orientation is hardly used in connection with this class of experiment in the same sense as that employed by physiologists. There is a distinction, not however always easy to draw, between orientation and power of direction.

Forel summarises his views in the following terms: "The faculty of orientation outside the body itself of the individual rests neither in a special mysterious force nor in an unknown sense, static, geotropic, or other, nor in a sixth sense, nor in the semicircular canals. It is the result of the experience of known senses, combined or not, especially of sight and smell, according to the case and the species. In aerial orientation it is vision which most predominates. The case of the carrier-pigeon constitutes the most surprising case of aerial orientation. Since it is explained by vision, it is idle to search in the domain of other mysterious causes. In terrestrial orientation the sense of smell often plays a predominant part, but gives place to sight in many animals, among which are man, monkeys, arboreal reptiles, certain insects, etc. In the orientation of subterranean and cave-dwelling animals, smell and touch reign as masters. In spiders it is touch which is the principal orienting sense."[2]

There seems to me little doubt that Forel's assertions are too sweeping. As Bonnier has noticed, we can trace in the animal kingdom a series of organs consisting when reduced to the simplest terms of a solid particle suspended

[1] *The Senses of Insects*, by A. Forel, trans. by M. Yearsley. London, Methuen, N.D., p. 214.

[2] Forel, *op. cit.*, p. 242.

in a liquid. The simplest type, found in certain jelly-fish (Fig. 3), is a tentacle which has lost its suppleness and mobility and acquired a considerable freedom of inertia. We then come to a modification consisting of calcareous particles (otolithic organ, Fig. 4) suspended more or less freely. Eventually we reach a degree of specialisation at which the otolith is lodged in a separate cavity containing a fluid distinct from that which bathes the animal as a whole (Fig. 5). Numerous experiments, some of which will be described, tend to prove that the homologues of these organs in the higher mammals and in birds are really connected with the faculty of equilibration; it is tempting

FIG. 3.

FIG. 4.

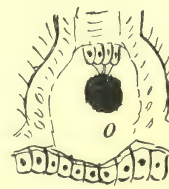


FIG. 5.

to postulate a similar function in the case of animals, experiments upon which are difficult both to plan and interpret.

In the case of man, while it may be freely admitted that the other senses, especially that of sight, generally modify and can, to some extent, replace the special sensory organs of equilibration, the importance of the latter are unquestionable. Many writers distinguish carefully between the equilibrating sense and the perception of muscular movement. Such a distinction looks well enough on paper, but hardly corresponds to anything found by experiment. I shall therefore not attempt any strict classification, but describe the best ascertained facts, subsequently touching on the more important theories which have been proposed to cover them.

Let us first consider sensations of position referred to a vertical axis. For these investigations the subject is fastened in the dorsal decubitus, on a plank capable of rotation round

a horizontal axis (Fig. 6). The subject's eyes must be closed and care taken to minimise the information derivable from cutaneous sensations due to sliding or changed pressure on the soles of the feet as the plank is rotated. The subject's knowledge of his position is tested in a simple way. After he has been rotated a certain amount, he is made to hold a light rod in what he thinks to be a position at right angles to the true horizontal—*i.e.* vertically.

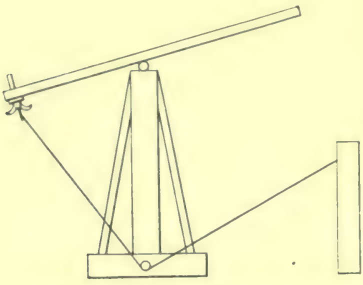


FIG. 6.—Diagram of Plank Bed capable of Rotation Round a Horizontal Axis.

Delage and others have found that rotation through an angle of 60 degrees is correctly estimated. Less degrees of rotation are under- and greater amounts over-estimated. Bending the head forwards increases the error up to 60° and diminishes it between 60° and 90°. Analogous results are obtained when rotation is made round a sagittal axis. As before, the position of the head is important. Thus Sachs and Meller found that if the head be fixed vertically and the body inclined, the inclination is over-estimated; if the body be vertical and the head inclined, the opposite result is obtained.

Next as to the relation between the sense of position and optical orientation. If a straight line be ruled on a vertical screen, its inclination to the true vertical can be estimated with considerable accuracy. Roughly, an inclination of 1 degree in a line 40 centimetres long seen from a distance of 2 metres can be detected. If the head be rotated, or the whole body, on a sagittal axis, a really vertical line appears to be bent in a direction opposite to that of the body movement (Sachs and Meller, Aubert). The presence in the field of vision of objects known to be vertical causes the disappearance of this and kindred illusions. If, on the other hand, the eyes be directed to a horizontal plane, *e.g.* the ceiling, when lying on the back, judgment of direction is far less efficient. Generally, the assumed principal horizontal axis of reference, with

respect to which inclinations are judged, coincides with the long axis of the body, but such concepts are far less accurate than those of position in a vertical plane. Evidently these experiments suggest that the equilibrating organ is influenced by gravity.

When the body is moved without altering its objective relation to the vertical, various illusions are produced. It is well known that from an express train moving round a curve houses bordering the line appear bent towards the carriages. The interpretation of this is, however, not free from difficulty, and less equivocal observations have been made. In rotation round a vertical axis, in an experimental modification of a "merry-go-round," the true vertical is judged to be inclined, and a plummet which has taken up a position due to the resultant of the two forces, the vertical component of gravity and the angular horizontal rotatory force, is judged to be really vertical; for instance, a pendulum will take up a position depending on the magnitude of the resultant of these two forces and appear to be vertical (Purkinje). The bearing of these results and their agreement with those detailed in the last paragraph is clear. It is also noteworthy that the illusion is not found in many deaf mutes (Kreidl). These are the main data regarding the sense of position as a whole. We next turn to the sense of position of separate parts of the body.

It would seem that normal persons form more accurate judgments as to the position of parts of the body which can be seen than of those, judgments regarding which are, uncontrollable by visual impressions. Thus, while our judgment as to the degree of flexion or extension of the fingers is good, we are often at fault respecting the toes, and still oftener in the case of the tongue. This is not, however, entirely a matter of visual memory, since the blind form quite accurate conclusions as to the attitude of their fingers. It is also not a matter of cutaneous sensibility, since cutaneous anæsthesia does not abolish the power. Deep anæsthesia, as in a patient thoroughly investigated by Strümpell, abolishes the sense of local position almost entirely.

Sensations of movement of the whole body have been

examined in detail. For the experiments to be pure, it is of course necessary that the subject should remain quite passive. Roughly speaking, we can classify the experimental results into those dealing with rectilinear and curvilinear motion. In the former case, uniform motion produces no sensation, only negative or positive acceleration; in the latter class an illusion of motion in the opposite direction may be produced. In ordinary life the presence in consciousness of the effects of other sensory stimuli hinders the development of distinct illusions, but even during uniform motion a change in the relative positions of head and trunk gives rise to a sensation of movement. It is also found that the subject's axis must be inclined in a direction determined by compounding the force producing rotation with the vertical component of gravity in order that he may appear to be vertical. If rotated in the true vertical position, the subject will think his body is inclined. These illusions are of course particular cases of those discussed in the previous section.

Another example is the observation of Yves Delage, that in swinging the inclination of the plane in which the swing is moving is only correctly appreciated when the head is vertical; if the latter be inclined to the right, the plane appears tilted to the left. The results of experiments on the movement of individual parts are precise enough to be formulated under four headings:—

1. The sense of movement is not necessarily greatest in those parts the position of which is most accurately judged. The movements of the toes are as well appreciated as those of the fingers—I speak of course of passive movements.

2. The sensibility partly depends on a succession of tactile excitations, partly on afferent impulses conducted by the centripetal fibres of muscles, tendons and joints.

3. Practice is markedly important. Loeb, Ostermann, and others have shown that in right-handed persons if the right and left hands be passively moved through the same distance, the subject invariably fancies the left hand has executed a greater movement. An opposite result is obtained in left-handed people.

4. Cutaneous anæsthesia does not abolish the appreciation of active movement, but the passage of a faradic current through the joint at which movement occurs wholly or to a large extent disturbs the accuracy of judgment (Goldscheider).

Akin to but not identical with the sense of local movement is that of resistance. That the sensation produced by pushing against a stiff indiarubber ball is not merely a mixture of tactile and "movement" impulses is shown by the facts that such sensations are produced when no movement takes place, and also when the skin is anæsthetic. Goldscheider's paradoxical experiment is another proof. If one lowers a weight attached to a string until it touches the ground, the sensation does not disappear immediately after contact with the floor, but one has the illusion of the string being replaced by a solid rod. This is perhaps due to the maintenance for a fraction of time of tension in muscle, tendon, and string.

The old idea that sensations of movement are "innervation sensations," a sort of automatic register of outflowing "motor energy," cannot be maintained. The evidence both of experiments and clinical observations demonstrates that an intact centripetal nexus is a *conditio sine qua non* of the sense. At least two sets of end organs can reasonably be regarded as the chief sensory elements in the process, viz. the muscle and tendon end organs. Perhaps the joint end organs are somewhat more important, because (1) movement is almost always localised in the joint itself, and (2) faradisation of the joint much dulls the sense. It cannot, however, be said that either consideration is decisive. That the sensation of resistance is an affair of tension seems probable from the Goldscheider paradox; perhaps the tension stimulates mechanically the end organs associated with the centripetal fibres connected with tendon bundles. I do not think any very conclusive evidence exists as to these points.

We now come to the practically interesting questions of vertigo and the so-called rotation reflexes. Vertigo is a term used to describe two different phenomena, viz. the sensation produced by looking down from a great height, and an illusion

of movement either as occurring in the subject himself or in surrounding objects. Vertigo in the latter sense alone concerns us here.

Although the definition anticipates the results of experiments which I have not yet described, we can best regard vertigo as that sensory condition which is induced when the information derived by consciousness from the labyrinthine organs is in conflict with that obtained through other sensory channels. All or any of the following antecedents may produce vertigo:—

(1) Rotation of the body.

(2) Movement in a curved path, especially rapid oscillation.

(3) Passage of a galvanic current through the head.

(4) Local cerebral injury, especially abscess.

(5) Cerebral anæmia, as in ordinary syncope.

(6) Certain poisons, particularly alcohol and tobacco.

(7) Any interference with binocular vision.

(8) Conflict of visual and other sense impressions.

(9) Disease of the internal ear.

This list could easily be extended.

With reference to rotatory vertigo, it is clear that the direction of apparent movement depends upon the position of the head during the previous rotation. The reader can easily satisfy himself of the truth of this statement by turning round sharply a few times with the head in different positions. If during the rotation the head be held in the ordinary erect posture, "things go round" in a horizontal plane; if the head be dorsi-flexed and then brought back into the vertical at the end of rotation, objects turn in a vertical plane.

Rotatory vertigo is not present in many deaf mutes. James found that of 519 deaf mutes tested, 186 experienced no rotatory vertigo, while this was present in 100 per cent. of 200 normal persons similarly examined. It is unnecessary to examine the other forms of vertigo in detail; they all depend, as a little reflection will convince the reader, on a conflict between the afferent impulses arising in our various intelligence departments.

Among the correlates of a change in the bodily posture, rotatory movements of the eye-ball have attracted special notice. The table contains some of the observations made recently by W. Nagel.

NAGEL'S EXPERIMENTS

Angular Rotation of Head	10°	20°	30°	40°	50°	60°	70°	80°	90°	100°
Compensatory Rotation of Eye-ball	1·3°	3·8°	5·2°	5·4°	6·3°	6·7°	6·8°	8·0°	8·1°	8·6°
Amount of Compensation	$\frac{1}{7 \cdot 7}$	$\frac{1}{5 \cdot 2}$	$\frac{1}{5 \cdot 8}$	$\frac{1}{7 \cdot 4}$	$\frac{1}{7 \cdot 9}$	$\frac{1}{9}$	$\frac{1}{10 \cdot 3}$	$\frac{1}{10}$	$\frac{1}{11 \cdot 1}$	$\frac{1}{11 \cdot 8}$

It would appear from the experiments of Delage that the amount of compensatory rotation is not the same for equal degrees of rotation to right and left. A similar process occurs when the head is rotated round a transverse axis. These eye movements are closely associated with the horizontal nystagmus which is observed when the body is rotated.

I have now described the chief general experiments dealing with the sense of position and movement; the more specialised researches which are concerned with theories of equilibration will be examined in the next chapter.

BOOKS RECOMMENDED FOR FURTHER STUDY

A. Forel, The Senses of Insects, translated by M. Yearsley. London, Methuen.

P. Bonnier, L'Audition. Paris, 1901, Doin.

W. Nagel, Die Lage-Bewegungs- und Wiederstandsempfindungen, Nagel's Handb. der Physiol., Bd. iii. p. 734. Braunschweig, 1905. (This memoir gives sufficient indications to enable the reader to consult the enormous literature of the subject.)

CHAPTER VII

THE SENSE OF POSITION AND MOVEMENT (*Concluded*)

Flourens, in 1828, first announced that injury to the semicircular canals is associated with disturbances of equilibration. Numerous observers have confirmed and extended his results, so that we possess a wealth of details respecting the changes which follow experimental interference with any part of the labyrinth, although theoretical interpretation is not in all cases beyond dispute. I do not propose to recapitulate more than a few of the chief researches; the works cited at the end of this chapter will help the student to a wider knowledge of this interesting field of observation. It may be said that no branch of experimental physiology has been more fruitful in producing new and ingenious methods of investigation, and that research in this direction is only profitable in the hands of those gifted with special aptitude for delicate manipulations.

Ewald found that extirpation of the labyrinth in pigeons produced muscular weakness, some uncertainty in movement—but not necessarily ataxia—and abolished the power of flight. One-sided removal caused frequent rotation of the head towards the operated side and irregularity in progression, but the power of flight remained. There was also unilateral muscular weakness. In frogs, muscular weakness is associated with bilateral ablation of the labyrinth (Schrader). After unilateral destruction, the muscular weakness is not marked, but there is rotation of the head towards the operated side and a tendency to curvilinear springing. In all animals investigated, compensatory eye movements cease to occur after destruction of the labyrinth. The exact relation of the labyrinth to general muscular tone is not, for obvious reasons, well understood.

The results of experiments on individual canals are quite

definite. Unilateral destruction of a single canal produces little or no effect, but when the corresponding canals of both sides are destroyed—*e.g.* in doves—pendular movements of the head in the plane of the affected canals generally occur. If one canal be stimulated in the *ampullary* region, the head moves in the opposite direction (Ewald, Breuer, Lee), but this does not occur if the ampulla be anæsthetised with cocaine before stimulation. Lee carried out exhaustive experiments with the dog-fish. He ascertained that if the fish were passively rotated round different axes, compensating movements of the eye-ball and fins took place. If the fish were rotated in the plane of a semicircular canal, exactly the same movements of the eye-ball followed as were produced by stimulating the canal in question. The same physiologist divided the animal's auditory nerve on one side and noticed rolling movement round the longitudinal axis towards that side. If both nerves were cut, no power of static equilibrium was retained, and the fish would lie indifferently on its back, belly, or side, and swim in these positions. He stimulated the ampulla of the anterior semicircular canal and noticed an upward rotation of the eye on the same side and a downward rotation on the opposite side. If the nerve were divided, the opposite result was obtained; if the nerves of both anterior ampullæ were divided, the fish dived downwards. On section of the nerves of both posterior ampullæ the fish swam upwards, sometimes putting its head out of water. These results hardly leave room for doubt as to the participation of the canals and labyrinth in the equilibration process.

Clinical evidence, on the whole, tends to support the conclusions drawn from experimental work, but, as seems generally true for sense physiology, the observations are not definite enough to have great importance attached to them. Most of the cases are connected with the symptom complex known as Menière's diseases and the pathology of deaf mutism. In the former condition, leading characteristics of which are vertigo and defective equilibration, disease of the labyrinth and canals has often been found. In deaf mutism, some good work has been done. Myguid found in 118 autopsies

on deaf mutes that 80 exhibited pathological changes in some part of the labyrinth; of these, 40 per cent. were cochlear and vestibular anomalies, and in 56 per cent. the semicircular canals were affected. It is a suggestive fact that disorders of equilibration are not invariably noticed in deaf mutes. Kreidl found that the normal horizontal nystagmus observed during rotation round a vertical axis was absent in 50 out of 109 cases of deaf mutism examined. The results of James were mentioned in the last chapter.

It only remains to sum up the attempts which have been made to resume in a general theory the facts of experiment and observation. Goltz originally suggested the hypothesis, that the endolymph excited afferent nerve endings by pressing more strongly on different parts of the labyrinth in accordance with the situation of the head. Breuer, however, pointed out that this explanation could only hold if the membraneous labyrinth were suspended in a compressible medium, such as air, and that it actually floats in the incompressible perilymph. The theory which resumes a majority of the facts is that due to Breuer, Mach, and Crum Brown.

Mach schematised the essential conditions of the problem in the following way: "Suppose in a body B there is a cavity on the walls of which there are nerve endings, and that this cavity contains a solid or liquid A. By its weight A will exercise a greater pressure on one part of the walls of the cavity than on the others, and it will thus determine the position of the body B relative to the vertical. With each acceleration of B, A will press in the opposite direction, and this contra-pressure will be added to the acceleration due to weight, so that the direction of the pressure as well as its intensity will change in the cavity. In like manner, with each angular acceleration communicated to B, A will oppose a rotation in the opposite direction. Thus B will obtain knowledge both of its position and of its progressive acceleration in a straight line, and, in the case of rotation, angular acceleration will also be indicated. The vestibule and semicircular canals in Mach's scheme constitute B, the vestibule possibly having to do with the sense of acceleration of movement in a straight line, while the semicircular canals serve for angular accelera-

tion. Each excitation produced in this manner . . . will give rise to a sense of rotation."[1]

Or, the matter can be looked at in a slightly different way. Suppose the three canals full of liquid, a rotation of the head in one direction will cause currents of fluid in the opposite direction owing to the liquid's inertia, and the amount of flow in each canal will depend on the plane of rotation. The crista of each ampulla is furnished with cells possessing hairs or cilia, and these cells are in close relation with afferent nerve fibres. It is not difficult to imagine that a back current in the endolymph will excite the hair cells, and through them the afferent fibres. In some such fashion might arise a sensation of movement in the plane of the canal and in a direction opposite to that of the actual movement. If the movement continue, friction will soon arrest the eddy; but if motion be suddenly stopped, the liquid will tend, for the previous reason, to continue flowing in the direction of former movement, and another sensation will be induced. The several hypotheses of Mach, Breuer, and Crum Brown differ in minor points, but are all of the above type.

The actual dimensions of the semicircular canals are such that no actual streaming of the liquid can be supposed to occur. This does not in any way invalidate the reasoning on which the Mach-Breuer theory is based, since there must evidently at each positive and negative acceleration be a change in the existing fluid pressure relations. In general terms, one may conclude that the Mach-Breuer theory describes satisfactorily the chief experimental data. Thus we should expect to be able to perceive accelerations, but not be conscious of uniform movement. Further, if any bending of the ampullary hairs in one direction call up a sensation of movement in the opposite direction—this is, of course, an *assumption*—we can understand the genesis of movement in the opposite direction which is associated with negative acceleration.

Of workers who decline to accept the hydrodynamic theory of Mach, Breuer, and Crum Brown, the most industrious

[1] J. G. McKendrick and A. A. Gray, *Schäfer's Text-book of Physiology*, Edinburgh, 1900, vol. ii. pp. 1200–1.

is Cyon. According to Cyon, the planes of the semicircular canals form a system of physiological co-ordinates to which we refer all our notions of space. Illusions of position which occur when the head is inclined are due to the altered position of these planes of reference. Cyon has written at much length on these questions, and his methods of controversy, which not infrequently take the form of offensive personal attacks on those who have the temerity to differ from him, are not calculated to secure unprejudiced consideration of his views. Nagel writes: "The way in which Cyon supposes the system of canals to act as a source of the conception of space is not, as I must frankly admit, intelligible to me; for this reason I am compelled to abandon a closer investigation of his theory—if one can use that term."[1] I confess to being in the same state of mental confusion as Professor Nagel.

The sense of position as distinct from movement is *perhaps* referable to the end organ of the utricle. The sensory epithelium of the utricle differs from that of the semicircular canals in having a mass of small solid particles (otoliths) applied to the hairs. It is clear that with varying degrees of rotation of the head the extent to which the hair cells are pulled on by the otoliths will be altered; it is also evident that so long as the new position is maintained, the stimulation will endure. This mechanism therefore, unlike that of the semicircular canals, provides for a long-continued excitation, and would be a basis for the origin of general sensations of position. The theory, although by no means free from objection, is perhaps the best at our command. It is also possible that the utricular end organ gives rise to sensations at the beginning and end of motion in a straight line, but here we are on very unsafe ground, and the question must still be regarded as quite an open one.

[1] Nagel's *Handb. d. Physiol.*, vol. iii. p. 804.

BOOKS AND PAPERS RECOMMENDED FOR FURTHER STUDY

Flourens, Mém. Acad. d. Sciences de l'Instit. de France, 1828, ix. 5.

Lee, Journ. Physiology, xvii. 192.

Mach, Grundlinien der Lehre von den Bewegungsempfindungen. Leipzig, 1875.

Crum Brown, Journ. Physiology, viii. 327.

Breuer, Med. Jahrb., p. 72. Wien, 1874–5.

**Nagel*, Handb. d. Physiol., Bd. iii. p. 734.

**McKendrick and Gray*, Schäfer's Text-book of Physiology, vol. iii. 1194.

**Sherrington*, ibidem, p. 1002.

Maxwell Labyrinth and Equilibrium. · 1923

CHAPTER VIII

HEARING—HISTORICAL SKETCH

IN previous chapters of this book I have described the sense organs from the point of view of a modern physiologist. References to the thought and work of a remote antiquity have been scanty, and the reader may well have been encouraged in the common and erroneous idea that the modern student can safely disregard that which was believed in olden times. My excuse is that information respecting the sense organs so far considered requires for its arrangement in proper historical perspective a wealth of space and mastery of antiquarian detail far exceeding my means. In the case of hearing and vision, this excuse will not serve. Professor J. I. Beare has, in his masterly treatise,[1] conveyed so intelligible an idea of the psycho-physiology of hearing and sight as interpreted by the Greek philosophers, that an ignorance of their language can no longer be pleaded in defence of neglecting their matter. I shall in this chapter summarise certain conclusions at which we may arrive in regard to this historical branch of psycho-physiology. The time is approaching when the student of natural science will be as ashamed to confess ignorance of the history of his subject as any educated man is to admit that he knows nothing of the history of his country.

The earliest writer as to whom we have explicit information is Alcmæon of Cretona. His view was that the air (vacuum) of the intra-tympanic region was the intermediary of hearing. This air catches up and reverberates an external sound, the reverberations being conveyed to the "point of sense," or interpreting structure, which is the brain. Alcmæon had got to the stage of recognising something

[1] *Greek Theories of Elementary Cognition from Alcmæon to Aristotle*, by John I. Beare, Oxford, 1906, pp. 354.

internal, an air-filled cavity, as a physiologically necessary organ. Empedocles went further. According to him, just as the organ of vision contains a lantern, the organ of hearing contains a bell or gong which is rung by the outer sound. Presumably this ringing is conveyed in some fashion to the "point of sense," and the perception of sound is awakened. Exactly what this gong-like body corresponds to is not certain; scholars differ in their translations of the word used, but the best opinion seems to be that something inside the ear is meant.

The obviously weak point of the theory was clearly noticed by Theophrastus, who observes: "Empedocles explains hearing by stating that it is due to intra-aural sounds. But it is strange of him to suppose that he has made it self-evident *how* we hear by merely stating this theory of a sound, as of a gong, within the ear. For suppose that we hear the *outer* sounds by means of this *gong;* by what do we hear *the gong itself* when it rings? For this—the very point of the whole inquiry—is neglected by him."[1]

It is a far cry to the days of Theophrastus, but succeeding ages have not produced a theory of hearing which will pass through his criticism unscathed.

The theory of Democritus has little physiological importance. He regarded hearing as a mode of contact between the atoms of sound and the soul atoms of the body.

Anaxagoras, again, did not advance the matter to any extent. The following sentences epitomise his theory: "Anaxagoras held that φωνή (vocal sound) is produced by the *breath* (or air in motion) which collides against the *fixed, solid* air, and, by a recoil from the shock, is borne onwards to the organs of hearing, just as what is called an "echo" is produced."

The views of Plato are somewhat difficult to summarise. There is no evidence that he was acquainted with the physiological anatomy of the ear, nor is it certain that Archer-Hind is correct in attributing to him a theory of the physical basis of pitch which approximates to that

[1] Beare, *op. cit.*, p. 97. [2] *Ibid.*, p. 104.

now taught. "He defines vocal sound as (on its physical side) air in motion, impelled from the seat of intelligence, through the mouth, and (as physiological stimulus of hearing) a shock caused by the air, through the ears, to the brain and blood, propagated to the soul."[1]

Plato, like his predecessors, seems to have believed that air was actually projected from the sounding body to the ear. It is, in Beare's opinion, doubtful whether the word *κινήθεις* can fairly be translated to mean "vibrations," since the conception of air as an elastic vibrant medium, in the modern sense, cannot safely be attributed to any of the Greek writers.

Many scholars, for instance Trendelenberg, maintain that a portion of Aristotle's writings on sound has been lost. Even from his undoubted works, however, we can construct a valuable account of the sense of hearing. In considering the physiological psychology of the senses as expounded by Aristotle, it is necessary to bear in mind certain leading principles. For Aristotle, the subject-matter of any sensory mechanism can always be regarded from two points of view, the actual and potential. In making this distinction, Aristotle often comes near to the standpoint of the modern physiologist who accepts Müller's law as, at least, a true principle. It will be seen that this dualism is predicated both of the physical "cause" or stimulus and of the physiological or psycho-physiological recipient. Beginning with sound, the "object" of hearing, a distinction is made between sound in general, including noises, and articulate sound which, although strictly applied to vocal sound, can be extended to any musical sounds, however produced. In sound, taken generally, we have its actual and potential aspects; some things, *e.g.* wool, cannot be made to produce sound, and are both actually and potentially soundless. Others, *e.g.* brass, are potentially sonant even when not actually giving rise to sound. "As it is possible for a person possessing the faculty of hearing not to hear actually at some given moment, so a thing may have the property of sounding without actually doing this. When, however, that

[1] Beare, *op. cit.*, p. 107.

which can hear realises its potentiality, and also when that which can sound does sound, then the realised faculty of hearing and the realised sound both concur; so that the former may properly be named 'actual hearing,' and the latter 'actual sounding.'"[1] The actualisation of potential sound depends on the existence of a medium, so that the whole process requires the co-operation of three things—an object, a receiver, and a medium. In the case of land animals the medium is air, and a *local* movement of it is essential. If there be a general or total movement, the necessary condition is not fulfilled, and no sound is produced. A boat on a river which moves because that in which it is fixed moves, produces no sound. The organ of hearing, the receiver, consists of air physically homogeneous with the external air, its peculiarity being that it is confined in a chamber so as to have a proper motion of its own. "Thus it has a peculiar resonance like a horn; and this, while it lasts, is a sign that the auditory faculty is unimpaired. . . . We can hear to some extent under water, because the water does not enter the air-chamber of the ear. If it did so, hearing would be at an end. Hearing ceases to be possible if the tympanic membrane is injured, just as blindness ensues if the membrane covering the eye is injured. As the water-holding eye is joined with the watery brain, so the air-holding ear is connected with the air-holding hinder part of the cranium."[2] Sound, physically considered, is a movement of something, and, unlike light, travels through the air; this is proved by the fact that we see a blow struck some time before we hear the sound.[3] Articulate sounds are due to the conformation of the air in motion, and are less well heard at a great distance owing to a blurring of this conformation. Pitch differences are only potential in the sound as a physical event, but are actualised in the sound heard. "The sharp is that which moves the sense much

[1] Beare, *op. cit.*, p. 112. [2] *Ibid.*, p. 115.

[3] "Sed tonitrum fit uti post auribus accipiamus,
Fulgere quam cernant oculi, quia semper ad auris
Tardius adveniunt quam visum quæ moveant res."
—*Lucretius*, vi. 164.

in a little time, the grave that which moves it little in much time." There is, however, a physical substratum for this, in so far that grave sounds correspond to slow and sharp sounds to rapid motion. It may be observed that Aristotle probably understood by motion actual translation of masses of air; we must not read into his statement our modern notions of pitch. Turning to the physiological anatomy of the ear, we have but vague indications as to Aristotle's knowledge of the matter. "One (viz. the inner) part of the ear is nameless, the other is called the 'lobe.' The whole consists of cartilage and flesh. Inwardly its formation is like that of spiral shells, the bone at the inner extremity (into which, as last receiver, sound comes) being in shape like the (outer) ear. This inner ear has no passage into the brain, but it has one to the palate, and a vein extends into it from the brain."[1] It would seem, from this passage, that Aristotle had examined the cochlea, but regarded the middle ear and cochlea as forming together one chamber.

A discussion of the biological and intellectual importance of hearing relatively to the other senses does not much concern sense physiology. The teaching of Aristotle in these respects might stand with little modification to-day. He points out that although the primacy among the sense belongs to vision if we regard the mere preservation of life, yet, for intellectual development, the sense of hearing is more important. This is because words are in their nature general, and to be regarded as the signs of ideas. "The impressions of sight, on the other hand, are primarily of the nature of particulars, and appeal rather to the individual. Those received from λόγος through the sense of hearing are, almost from the first, of the nature of universals, and therefore almost directly (*i.e.* so far as we *understand* them) stimulate the faculty of intelligence."[2] Aristotle, of course, pointed out that these results are secondary, that the *immediate* data of hearing, like those of every other sense, necessarily consist of particulars. A full discussion of these and kindred matters would be out of place in a physiological book, a

[1] Beare, *op. cit.*, p. 122. [2] *Ibidem*, p. 124.

remark which also applies to the subject of Greek harmonics. The above sketch will be sufficient to enable the reader to realise the importance and value of Greek physiological psychology. I must once more impress on him the necessity of examining his subject historically as well as experimentally.

RECOMMENDED FOR FURTHER STUDY

An adequate guide to the literature will be found in the work of Professor Beare, from which I have so frequently quoted.

CHAPTER IX.

PHYSIOLOGY OF THE EAR

SOUND, whether considered from the physical, physiological, or psychological side, has been the object of such close study in the last two hundred years, that our knowledge of many important phenomena is relatively minute. It is my intention, however, to deal with the problem in an even less detailed manner than has been the case with the other divisions of sense physiology. In my opinion, founded on the experience of some years' teaching, many of the most interesting researches on tonal analysis, the resonator theory of the cochlea, etc., can only be made intelligible to those having received a wider preliminary training in physical acoustics than I may assume to be the case with the reader of this book. It would, of course, be possible to supply this defect by writing a physical introduction to the subject, but to do so would force me to exceed reasonable limits of space and time. Not only am I convinced of the necessity of taking this course, but further, it happens to be one which can be followed with the least inconvenience to the English reader. Most of the classical writers on vision, for instance, can only be consulted by those who have been wise enough to acquire a knowledge of French and German. Helmholtz's great treatise on the physiology of the ear, a work which, altogether apart from the question as to how far the theories it promulgates may be correct, must be the starting point of a course of reading on the subject, has been translated into English. To this book, and to the others mentioned at the end of the chapter, the reader's attention is particularly directed; a perusal of this sketch cannot, and will not, give him an adequate idea of the profoundly interesting discoveries which have been the fruit of investigation.

From the physical standpoint, simple tones are pendular vibrations of the sounding medium, and their graphical representation corresponds to that exhibiting the change in value of the sine of an angle as the angle varies continuously. Such tones can differ one from another in at least two respects, viz. (1) the number of vibrations in a unit of time, (2) the amplitude of such vibrations. For reasons which will be more particularly referred to below, it is usually stated that sounds differing in the first way differ in *pitch*, and if the change be of the other kind, in *intensity*. In order that the ear may perceive a given note, the pitch and amplitude must lie within certain limits. The determination of the upper and lower boundaries of pitch is a matter of difficulty. Most of the earlier workers were unable to exclude the possibility of their results being vitiated by the presence of impure tones. Another point is that while, in the middle of the scale, overtones are feebler than fundamentals, in the lower region the reverse relation holds. There is some reason to think that vibrations at the rate of 15 per second cause a perceptible note. A somewhat analogous uncertainty holds with regard to the upper limit of pitch perception. Edelmann, using an improved form of the well-known Galton whistle, obtained an audible note having a frequency of 50,000 vibrations per second. The objection to such experiments is the fact that Galton's whistle does not appear to furnish a note of constant intensity.

We all know that tones in different regions of the scale possess a different character, or, to adopt a familiar German expression, tone colour. It has been laid down that, other things being equal, the intensities of two notes of different pitch are directly proportional to the kinetic energies of the respective moving masses.[1] Helmholtz, however, showed with a syren apparatus,[2] that when the same amount of mechanical work was expended in the production of two notes of high and low pitch respectively, the former appeared to be the more intense. Now, the kinetic energy or, what comes to the same thing, the mechanical work is proportional to $(an)^2$.

[1] Helmholtz, *Tonempfindungen*, English trans., p. 75. [2] *Ibid.*, p. 174.

where a is the amplitude, and n the number of vibrations in a unit of time. If this is to remain constant, n must decrease as a increases, hence when a is kept constant, the value will increase with n, and when two notes have the same amplitude but different pitches, the higher pitched note will be the louder. An objection to this method of proceeding is that loudness is subjective, and that it is very difficult to compare with respect to this character two notes of quite different pitches.

The determination of the minimum amplitude of vibration corresponding to an audible note is a matter of practical importance, as it affords a criterion of the normality, or otherwise, of the subject's hearing powers, and is largely used by aural surgeons. Many methods are in use, of which that originally proposed by v. Conta appears to be the most satisfactory. It has been shown by Wead that the kinetic energy of a vibrating tuning-fork is equal to $\frac{bd^3E}{8l^3} \cdot a^2$, where l is its length, d its thickness, b the breadth of the prongs, a the amplitude of vibration, and E Young's modulus for steel. When such a fork has been set in vibration, its energy falls off in a manner dependent solely on the amplitude. Thus it can be shown, by reasoning based upon Laplace's equation for small oscillations, that if at any instant the amplitude is a_o, t seconds later the amplitude is $a_o\frac{1}{e^{ht}}$, where e is the Napierian base, and h is a constant.

Now, writing Wead's equation in the simple form $V = Fa^2$, t_p secs. is after the fork has been started $V = F\,(a_oe^{-ht_p})^2$. A certain fraction, say $\frac{1}{n}$, enters the auditory meatus of the subject. Therefore, if he can just hear the fork, his threshold intensity $Ip = \frac{F}{n_1}\,(a_oe^{-ht_p})^2$.

Now, supposing a deaf man can still hear the fork after the shorter period t_q. Then his threshold intensity Iq is $\frac{F}{n_1}(a_oe^{-ht_q})^2$. But if both normal and deaf listened under approximately the same physical conditions, $n = n_1$, hence

$\frac{Ip}{Iq}=\frac{(a_0e^{-ht_p})^2}{(a_0e^{-ht_q})^2}=e^{-2h(t_p-t_q)}$, or the deaf person's auditory acuity $\frac{1}{Iq}=e^{-2h(t_p-t_q)}\times\frac{1}{Ip}$. Of these quantities, h can be ascertained by experiment for any given fork, t_p and t_q are found in the examination of the subject and control. It is apparent that to render the process at all accurate, many normal persons must be examined under approximately the same physical conditions, and that a tuning-fork is not an altogether satisfactory instrument. Marrage, three or four years ago, introduced a syren for testing purposes, but I do not know whether it has, in practice, proved more useful than the tuning-fork method. In any experiment it is of course necessary to exclude so far as possible all extraneous sounds, and it is of some interest to know whether all such sounds are equally disturbing. The experiments of Mayer, partly confirmed by Stumpf, suggest that low pitched notes produce, within certain limits of intensity, more marked interference in the perception of high notes than do the latter on the perception of the former. These disturbing influences naturally become more important as we approach the limen. Absolute silence, indeed, cannot be realised, and the absolute threshold value cannot be measured. When all external noises are hushed, we hear the beating of our arteries and the sound of our breath, etc. In order that a note may be perceived at all, not only must it possess a certain vibration frequency and a certain intensity, but it must endure for a finite time. This can be experimentally studied by means of an apparatus so arranged that the note of, *e.g.*, a tuning-fork is allowed to reach the ear through a tube which can be automatically opened and closed very quickly. Numerous workers have tackled this problem, and it seems that two vibrations of a tone vibrating at the rate of 72 per second are sufficient to set up a corresponding tone sensation (Pfaundler, 1878). Abrahams and Brühl, who employed a syren, assert that while two vibrations are sufficient in the middle of the scale, the necessary number increases steadily as the pitch rises. This is, of course, exactly what one would expect.

Passing to the subject of compound notes, only a few

sentences can be devoted to the physics of the matter. A compound note, *e.g.* a simple harmony, or the air movement produced when a violin string is bowed, consists of a fusion together of the effects produced by each individual component. This fusion is of such a nature that the individual constituents can be recovered from the mixture either (1) Experimentally; thus if three tuning-forks vibrating at the rates of 100, 200, and 400 per second respectively blend to form a single compound movement of the air, then three tuning-forks having the same vibration frequencies as those of the blending instruments set up on resonance boxes in the neighbourhood will each be set in motion. This is called sympathetic resonance. (2) If the form of the wave motion representing the compound tone is given, it is always possible to analyse this compound into simple constituents. This is called harmonic analysis, and its development is owing to the investigations of the mathematical physicist Fourier.

One of the chief objects of modern work has been to ascertain whether the facts of tone sensation suggest or are consistent with the existence of some physiological mechanism which can analyse sounds, as is done by a collection of tuning-forks or resonators in the presence of a compound note. An important limitation must at once be observed. Suppose we could show that those characters of a sound which we hear are precisely the ones which produce a physical effect on resonators, we should still have advanced only a little way in the physiological and not at all in the psychological description of the process of hearing. We should still have to answer, and fail to answer, the question of Theophrastus, that the gong may be rung by the outer sound, but what is it that hears the gong? This is of course recognised by all investigators; the reason why so much labour has been devoted to finding *analogies* between the process of sound reception and sympathetic resonance is, that some such method of reception would afford the simplest explanation for the elaborate structures of the internal ear which, all agree, are intimately connected with the process.

Bearing these important but frequently forgotten facts in mind, we may sum up the results of modern work in the following terms:—The analysis of a compound note which is effected by a set of resonators can also be carried out by the human ear, although the power of doing so and the attention requisite to distinguish the partials vary much from subject to subject. The fundamental work was done by Helmholtz in 1859. Helmholtz selected for study the vowel sounds of human speech because they can be produced as evenly sustained musical notes. While the accuracy of these conclusions has been generally admitted, some discussion has arisen as to whether any tonal phenomenon can be detected by the ear which does not affect a set of resonators. If one thinks for a moment of what happens in a sonant medium, for instance the air, when a sound is produced, one notices that there is a regular production of condensations and rarefactions graphically represented by the crests and troughs of the "waves" of a sine curve or on the figure traced out by a piece of stiff paper attached to the prong of a tuning-fork and writing on a uniformly rotated drum. Supposing one takes a tuning-fork vibrating at the rate of 100 per second, there will be in each second one hundred such crests and the same number of troughs. If now a second tuning-fork, also vibrating at the rate of 100 per set, be thrown into vibration a two hundredth of a second later than the first, then the crest of a wave in the first set of vibrations will always be accompanied by a trough in the second set and *vice versa*, so that if the two sets of vibrations have the same amplitude of vibration, the rarefaction phase of one will be counteracted by the condensation phase of the other, no movement of the sounding medium will be produced, and no sound will be heard. The two waves are said to be in a state of phase opposition, and the result is said to be a case of total interference. If instead of two forks of the same vibration rate set in motion consecutively we take two forks, one vibrating at 100 and the other at 101 per second, and start them together, then once, and only once, in each second the trough of one wave system

exactly corresponds to the crest of the other set, and the result is that a weakening in or cessation of the even flow of the sound is produced once a second. This phenomenon is called a beat.

Now with regard to the phase of a note, some physiological difficulty has arisen. It is, so far as a resonator is concerned, quite immaterial whether aerial motion which excites it begins by a phase of condensation or by one of rarefaction, but it is not equally clear that the ear cannot distinguish the two cases. In simpler language, it is doubtful whether the ear can or cannot distinguish between a push or a pull applied to the tympanic membrane. As a result of certain experiments by Lord Kelvin, experiments which are too complicated to be described here, it used to be taught that the ear can distinguish differences of phase. Recent opinion has not on the whole tended to accept this view. Lindig, for instance, has apparently demonstrated that Lord Kelvin's results cannot be applied to pure harmonies, that in such no alteration of timbre is produced by total reversal of phase relations.

Another phenomenon which appeared to be inexplicable on the basis of sympathetic resonance was that of beat tones. If the difference in frequency of two forks be continuously increased by filing one of them, the number of beats of course increases steadily. It was said that when the difference in frequency is sufficiently great, these beats themselves fuse into a note which is perceptible to us but does not excite a physical resonator. The researches of Helmholtz,[1] Schaefer, Hermann, and others seem to have demonstrated that these so-called beat tones are really examples of combination tones occurring under special circumstances. The genesis of a combination tone is theoretically simple enough. If two forks having vibration rates of 200 and 400 per second respectively are set in motion, in addition to the compound wave generated by their fusion

[1] Helmholtz's views will be found on pp. 156 *et seq.*, *op. cit.* A mathematical investigation is given at p. 411. The older literature is collated at pp. 527–535. Recent work is discussed by Schaefer, *Nagel*, vol. iii. pp. 552 *et seq.*

a component is found which has a vibration rate equal to their difference, namely, 200 per second, and another with a frequency equal to their sum, namely, 600 per second. The former is called a difference and the latter a summation tone, and the whole class of such tones is termed a group of combination tones. Now such notes correspond to physical realities, and can, under certain conditions, excite resonators. It is thought that the so-called beat tones are akin to these combination tones, and that their reception by the auditory apparatus does not require us to postulate the existence of a mechanism different from that of a sympathetic resonator. I speak, however, with much reserve on this point. The subject of combination tones is a very difficult one to master. I am not at all sure that I understand the true bearing of the work which has been done, and am quite sure that my knowledge of physical acoustics is far too elementary to allow me to make the subject clear to my readers. I must therefore be content with the remark that, so far as one can judge, there is not at present any good reason for holding that tones which do not or cannot affect a physical resonator affect the receptive apparatus of the inner ear.

We must now, having considered the facts in a general way, examine briefly the physiological anatomy of the ear. Right up to the internal ear the meaning of the various structures is fairly easy to understand; at that point we become a prey to theories.

That the auricle acts as a reflector, directing the waves into the external meatus, is a reasonable supposition. Some two centuries ago Boerhaave attempted to prove that the pinna behaved like a parabolic reflector, but this was shown long ago by Savart to be erroneous. A method of investigation is to sound a compound note and observe whether its quality changes in accordance with the position of the source of sound in relation to the meatus. Sylvanus Thompson pointed out that the tick of a watch has a slightly different quality when the watch is held in the middle line behind the head from what obtains when it is held in the middle line and the same distance in front of the ears. The exact cause of this is, however, doubtful, and we know—from the experience of

times when clipping the ears was a recognised method of political argument—that removal of the pinna is a more serious detriment to one's personal appearance than to the sense of hearing. The external auditory meatus may also, in virtue of its curvature, possess some slight value as a resonator in the case of high pitched notes, but its protective function is clearly more important. This protective function is exercised in virtue of two characters, (1) the varying curvature, (2) the secretion of cerumen. The curvature renders it difficult for foreign bodies to impinge directly upon the membrana tympani, and the aromatic odour and bitter taste of the cerumen probably deter insects from taking up their abode in an inconvenient situation. The movements of the auricle are, in man, of little or no importance to the sense of hearing. The membrana tympani, as the reader will remember, is composed of two sets of fibres circularly and radially arranged, the former making an external ring. The tension of the membrane is maintained by the tensor tympani, the tendon of which is inserted into the handle of the malleus a little below the horizontal axis of rotation of that bone, so that it must exert an almost constant degree of traction on the membrane. The form of the membrana is conical, but the walls of the hollow cone are convex outwards, owing to the disposition of the central fibres. Had the membrana been a uniformly stretched membrane like a drum-head, the amplitude of its movements must have steadily increased from within outwards, but the peculiar structure avoids this, together with the weight of the malleus; in addition to this, the arrangement of the radial fibres affords a special functional advantage. These fibres, as we have seen, are slightly convex externally, but their curvature is very slight. Helmholtz[1] pointed out that the curvature being very slight, small variations of it would be associated with relatively large excursions of the centre of the fibre in a plane at right angles to their direction. The consequence is that very slight changes in air pressure in

[1] Helmholtz, *Tonempfindungen*, etc., English trans., p. 135. The proof is given more fully by McKendrick and Gray (*Schäfer's Text-book of Physiology*, vol. ii. pp. 1154–1155).

the meatus will produce relatively great effects on the transmitting mechanism, the membrana tympani; that is to say, this special form of membrane secures the maximum degree of effect to sounds of feeble intensity. The action of the intrinsic muscles of the middle ear now deserves attention. We saw that the tensor tympani is so inserted that it maintains a constant tension in the tympanic membrane when the muscle is uncontracted or in a constant state of tone. When the muscle contracts it necessarily renders the membrane more tense, and is generally believed to damp loud notes by diminishing the excursion of the membrana. Some few persons can contract the muscle voluntarily, but generally the contractions are reflex, the arc being auditory nerve-brain-trigeminal nerve. It is certain that the contractions raise the intra-labyrinthine pressure, but the assumed damping effect is not satisfactorily proved. The action of the stapedius is still more doubtful. Henle was of opinion that the muscle held the plate of the stapes firmly in place, and prevented it being forced into the fenestra ovalis when strong pressures force in the membrana tympani. Pollitzer has given a different interpretation; according to him, the stapedius is to be regarded as an antagonist of the tensor tympani, drawing the foot-plate of the stapes out of the fenestra ovalis and, by releasing the tension of the chain of ossicles, producing relaxation of the tympanic membrane. It is asserted, but clinical experience is not quite concordant on the point, that paralysis of the facial nerve caused by pressure in the aqueduct of Fallopius is associated with increased sensitiveness to loud sounds.

The three auditory ossicles act roughly as a bent lever of the second order. The fulcrum is the horizontal axis of rotation of the malleus, the handle of the latter is the long arm, and the long process of the incus carrying the stapes is the short arm. The ratio of the arms is effectively 1·5 : 1, so that there is an increase in force and diminution in amplitude of movement. This arrangement is satisfactory when one remembers the far greater extent of surface presented by the membrana tympani than that of the membrane covering the fenestra ovalis. That most perceptible sounds are con-

veyed to the internal ear by this mechanism is shown by the serious effects on hearing accompanying disease of the middle ear, even when the internal ear is unaffected. Bezold, however, has made it probable that very high notes may be transmitted to the internal ear even when the ossicles are completely ankylosed together. Only one other structure in the middle ear needs mention, the Eustachian tube. The prime function of this canal is to enable the air pressures within and without the tympanic cavity to be equalised, but it is, as Mach and Kessel pointed out, of importance that the opening should be normally closed, since otherwise, owing to the fact that all parts of the head are affected by the wave of sound, the excursions of the tympanic membrane would be too much damped, it being, as it were, simultaneously pushed on both sides when the Eustachian tube is opened. The importance of the power of opening the tube for normal hearing is well shown by the effect on this sense of exposure to compressed or rarefied air. It may be remarked that under all high pressures the mere act of swallowing is not, in most cases, sufficient to open the tube; it is necessary to expire sharply with mouth and nostrils closed.

We now come to the structures of the internal ear, and the student who is not already familiar with the very complicated apparatus therein contained should consult one of the better text-books of histology or anatomy, since space only permits a brief reference to the matter here. The cochlea, which is undoubtedly an essential structure for hearing, is a convoluted tube wrapped round a central pillar, the modiolus, and divided into two cavities, the upper scala vestibuli and the lower scala tympani, by the lamina spiralis. The scala tympani abuts on the middle ear by the fenestra rotunda, which is covered by a membrane. The patency of this foramen is important, since if its wall becomes rigid the practical incompressibility of liquids makes it impossible for the stapes to move. The lamina spiralis is incomplete at the apex of the cochlea, where the two scalæ communicate by way of the helicotreme. A portion of the scala vestibuli is cut off by a special membrane, Reissner's membrane, and ends blindly below, communicating by a side channel with

the saccule. This section of the scala vestibuli is called the canalis cochleæ, and contains a series of complicated structures, consisting of (1) peculiarly shaped cells with hair-like processes, arranged in two rows; (2) tiny rigid structures arranged in pairs, the rods of Corti; (3) cells thought to be sustentacular; (4) a tectorial and a basement membrane, of which the latter is composed of fibres, the length of which varies continuously from apex to base of the cochlea, and which is closely associated with the ends of the cochlear division of the auditory nerves, the nerve endings being also in very close relation with the hair cells standing on the basement membrane. The structure of the cochlea varies in its fine details in different animals, and has been much elucidated by the beautiful preparations of Gray, whose work should be consulted.

The exact meaning of these elaborate structures has been much debated, and nothing like agreement as yet prevails; of the various modes of action suggested, the most ingenious and, in spite of various defects, the most plausible is that propounded by Helmholtz.[1] In the opinion of Helmholtz, the cochlea should be regarded as a vast congeries of resonators, composed of separate vibrators, each tuned to correspond to a single vibration period, and altogether containing enough vibrators to respond to all notes within the range of audibility, say from 15 to 50,000 vibrations per second. Each of these vibrators[2] is capable of exciting a nerve filament which physiologically "corresponds" to it, so that a nervous impulse "corresponding to" (*not* identical with, in any physical sense) the frequency of the vibrator is transmitted to the brain. The mass of each vibrator is such that its inertia is slight; it is easily set in motion, and easily brought to rest again. Damping arrangements exist in the cochlea which will quickly extinguish movements of the vibrating structures. The method of action is taken to be somewhat as follows. When a simple tone falls on the ear, there is a pendular movement of the base of the stapes and

[1] *Op. cit.*, pp. 142–152.

[2] It is known that structures somewhat analogous with the hair cells of the cochlea, found in crustacea, vibrate sympathetically.

the structures in the internal ear are set in motion, but any particular structure, the vibration period of which corresponds to that of the exciting tone, will be specially affected. A particular nerve filament is thus stimulated, a particular impulse is conveyed, and there, by processes utterly unknown to us, the sensation of a tone of definite pitch passes into consciousness. The loudness of the sound is supposed to be conditioned by the amplitude of movement of the cochlear resonator. When a compound wave of pressure is communicated to the structure of the inner ear it is analysed by the vibrators, the periods of which correspond to its partials, and all the impulses separated by the individual resonators pass to the brain as an imperfectly fused whole, which can by an effort of attention be again resolved into constituents, these psychic constituents "corresponding" to the separate excitations. It may be admitted that the cochlear structure affords, so far as the number of units which might be conceived to resonate, an anatomical basis for the theory, provided one takes the fibres of the basilar membrane to be the vibrators. There is also some experimental evidence consistent with the hypothesis. Exner and Pollak have recently shown that periodic phase variations (*vide supra*) affect the intensity of tonal sensations, just as they affect the intensity of response in sympathetic resonators. Numerous experiments have been performed on animals in which specified portions of the cochlea have been destroyed and deafness to certain notes has been asserted to occur. Deafness to certain parts of the scale, tonal lacunæ, has been frequently observed in man, and, in a *few* cases, post-mortem examination has revealed pathological changes in certain portions only of the cochlea. I believe this evidence is of little value, particularly the experimental portion. Not only is it extremely difficult to produce limited injury of the cochlea in small animals, but the examination of their auditory sensations cannot be carried out with sufficient exactness to lead to very definite results. Some evidence from the clinical side is, perhaps, rather more worthy of consideration. I allude particularly to the condition studied by Jacobson, and dignified with the awe-inspiring name of

Diplacusis binauralis dysharmonica, in which the patient hears with one ear a greater or smaller portion of the musical scale "falsely." Such a condition is easy to describe in terms of Helmholtz's hypothesis, difficult to account for on most of the others. Suppose on this theory that the *c* fibre in the left ear is pathologically changed in dimensions so that it vibrates to *d*. Then when *d* is sounded, the *d* fibre of the right cochlea responds with both the *d* and *c* fibres of the left cochlea, but the note associated with the *c* fibre is normally *c*, hence in binaural hearing the sensation of *c* will be erroneously associated with *d*, and dissonance results.

Most of the secondary phenomena of compound tones agree well with Helmholtz's hypothesis. Two tones near each other in pitch should excite a zone of fibres, and so lead to variations of intensity of the nature of beats; if the difference of pitch is great, the excitation of the intervening zone will not be marked enough to produce any effective disturbance of this nature. Both these deductions appear to be experimentally true (Stumpf). The question of combination tones and their relationship with the so-called beat tones has been mentioned above. I attempted, some years ago, to throw light on the theory by leading to each ear the same note, but so arranging the source of sound that the note reached one ear half a wave length later than the other. On the resonance hypothesis, this should produce almost total interference. I was in no case able to produce total interference, but merely to alter the localisation of the sound, although in some cases variations in intensity were noticed. I subsequently found that Sylvanus Thompson had previously carried out similar experiments with the help of a somewhat more perfect apparatus and a better arrangement. His results also failed to reveal any case of total interference, merely peculiar localisations of the sound.

The main objection to the theory is the extreme difficulty, in view of the histological structure, of understanding how the fibres of the basilar membrane can vibrate in the way postulated by Helmholtz. Pierre Bonnier has criticised the theory from this standpoint, and many of the objections he raises are formidable. Numerous other theories have

been proposed, some of which are highly ingenious. Those of Waller, Ebbinghaus, Hurst, Mayer, and Ewald, while assuming that cochleal analysis occurs, lay stress on variations in the form of the compound waves, and deny the existence of resonators in Helmholtz's sense. Ewald, in particular, has shown that sound waves produce peculiar patterns on oiled membranes of sizes comparable to that of the cochlea, and that different compound waves produce different patterns. He has published some interesting microphotographs in support of his views. Sir T. Wrightson and A. Keith have drawn attention to the peculiar conformation and articulation of the stapes, and are inclined to attribute to it a share in the process of tonal analysis. The theory of Rutherford, which transfers analysis to the cerebral structures, is, in effect, a confession of ignorance, and does not present any features of sufficient interest to need detailed examination. In my opinion, the theory of Helmholtz accounts satisfactorily for a greater number of facts than any of the others, but at the same time the difficulties in the way of its full acceptance are so numerous, that we must not regard it as an established truth.

The psychology of hearing, more particularly in relation to the theory of harmony and æsthetics, does not fall within my province to describe; the reader who has mastered the account of the matter contained in Professor Myers' admirable text-book should consult the other works mentioned below. I would once again remind him that the physiology and psychology of hearing, like most subjects of real interest, cannot be mastered without sustained attention, and that the works in question will require on his part strenuous application, which will, however, be amply repaid.

BOOKS RECOMMENDED FOR FURTHER STUDY

(The papers and memoirs dealing with the subject are too numerous to be referred to. The reader had better study the books mentioned in the order in which they are given.)

1. Text-book of Experimental Psychology, by *C. S. Myers*, London, 1909, especially pp. 20–62.

2. Die Lehre von den Tonempfindungen, etc., by *H. v. Helmholtz,* 5th edition, Braunschweig, 1896 (English translation by *A. J. Ellis,* with literature to 1885. London, Longmans).

3. Tonpsychologie, by *C. Stumpf,* two vols., Leipzig, 1883 and 1890.

4 Der Gehörssinn, by *K. Schaefer,* Nagel's Handb. d. Phys., vol. iii. pp. 476–588.

5. The Ear, by *J. G. McKendrick* and *A. A. Gray,* Schäfer's Text-book of Physiology, vol. ii. pp. 1149–1194. Edinburgh, 1900.

6. L'Audition, by *Pierre Bonnier.* Paris, 1900.

The histology of auditory structures is well described in *Dahlgren and Kepner's* Principles of Animal Histology, London, 1908, pp. 215–224.

CHAPTER X

THE COMPARATIVE PHYSIOLOGY OF VISION

ALTHOUGH it is idle to discuss whether any one of the sense organs is more or less important for the well-being of the organism as a whole than any other, yet if we judged by the bulk of relevant literature, pride of place would have to be assigned to the eye. This statement is true not only with respect to human but also in the case of general physiology, and I propose to discuss in the present chapter some problems of vision in animals other than man.

The powerful stimulus to the scientific study of natural history which we owe to the great biologists of the early and middle years of the last century, above all to Darwin, Alfred Russel Wallace, and August Weismann, resulted in the publication of numerous observations on the sense of animals, especially those of the social hymenoptera. In this field Lord Avebury, Forel, Plateau, and more recently Wassmann, have been especially active. The majority of their researches were directly or indirectly inspired by Darwin, and in general they may be described as the sort of work which Gilbert White would have performed had he lived to come under the influence of the biological renaissance. In other words, they are characterised by patient observation and the performance of comparatively simple experiments, the results being described in language as far as possible free from technicalities; comparatively little attention is paid to those minutiæ of structure which require for their elucidation somewhat elaborate training in the refinements of modern histology. It cannot be denied that the advantages of this kind of treatment, viz. an appeal to a large public and an encouragement of workers in conditions ignorantly supposed to be unfavourable to scientific research, are associated with certain weaknesses. Thus the reader will often notice a tendency to

somewhat facile generalisations and to the employment of a perhaps excessively anthropomorphic or anthropocentric method of interpretation. As generally happens, these shortcomings called into existence a school of opposite tendencies, a school the opinions of which are well expounded by Theodor Beer[1] and, more recently, J. P. Nuel.[2] The main thesis of this school can be summarised in a few words. Since no animal can attain to objective knowledge of the sensory and psychological processes taking place in any other animal, the study of sensations or of higher psychical processes depends on the interpretation of physiological reactions to stimuli.

In the case of man himself, the faculty of speech and the close agreement in structure found in individuals of the same race enable us to infer the existence in one another of sensations and other conscious states with some degree of probability. Still, even here we reason from similarities of anatomical structure and physiological reaction, so that errors frequently arise. Instances will readily occur to the student of medicine; thus stimulation of an afferent nerve causes (with one exception) a rise of blood pressure, and is normally associated with pain. Now this pain is a subjective matter, while the blood pressure can be objectively recorded; but we should greatly err if we asserted that the objective rise of blood pressure is an accurate indicator of the amount of pain felt. Again, when ethereal vibrations of wave length between 670 and 660 $\mu\mu$ strike the retina, some 96 per cent. of English adults experience a sensation which they all describe by the same word, red; the remainder, however, are affected in a manner which is not only different, but which the "normals" can by no effort of the imagination picture to themselves. If, therefore, under the most favourable conditions, viz. in the study of man by man, errors of interpretation occur, it is manifest that in dealing with animals, the anatomical and physiological characters of which differ from those of man in a way not to be mistaken, the attempt to

[1] "UeberPrimitive Sehorgane," *Wiene klinische Wochenschrift*, 1901, Nos. 11, 12, 13.

[2] "La Vision," *Bibliothèque Internationale de Psych. Expérim.*, Paris, 1904, Octave Doin, pp. 3–113.

place a conscious reaction, a sensation, side by side of a physiological response, is hazardous. We shall project outwards a more or less faithful picture of our own mental processes, and tend illegitimately to postulate the objective existence of that which is or may be subjective. To adapt Voltaire's taunt, we shall not merely fashion God in our own image, but the whole animal kingdom. For reasons such as these, Beer, Nuel, and their fellows hold that there is no such thing as comparative psychology, but only comparative physiology. They object to use in describing the senses of animals such words as "sight" and "vision," which they hold to be tainted by human associations. "Already the use of the words 'seeing,' 'vision,' gives rise to misunderstandings, for they presume the existence of a very complex organ and function, even a psychic representation, as in the case of man. To the word 'light' itself (employed to designate a form of energy) there adheres a sensorial after-taste which still continues to lead readers and writers into error."[1] A new terminology has accordingly been introduced which, at any rate, has the merit of being unfamiliar. Although we may admit that this group of physiologists has pointed out some important errors in the methods of the older writers, its adherents are perhaps less logical and consistent than they suppose. A characteristic of the whole school, to judge from Beer and Nuel's monographs, is a fine scorn of those who have been unfortunate enough to work in ignorance of the new terminological light, a scorn which not infrequently shows itself in somewhat meticulous censures. One illustration will suffice.

Professor Nuel writes: "Generally, the critical spirit of authors does not reach so far. They commence by admitting as an axiom the existence of sensations in an animal, and look on movements observed in it as incited by these sensations; that is to say, they set out from two gratuitous assumptions, as we shall see, to satiety later on. Thus Lubbock, to cite only one example, seeing that bees react differently to lights coloured differently (for us), concludes that 'the observations

[1] Nuel, *op. cit.*, p. 26.

demonstrate clearly that bees possess the faculty of distinguishing colours.' And, nevertheless, the observed facts could be just as easily explained by a simple difference in intensity of a single luminous sensation. But we shall see that even this single sensation is not demonstrated in the case of the bee by the experiments of the authors. The same writer, seeing that ants react to ultra-violet rays, draws the following conclusions: 'It is therefore probable that the ultra-violet rays produce in ants the sensation of a distinct colour, as different (for the ant) as is the green from the red (for ourselves).' He even asks himself 'if the white light of these insects is not different from our white, since it contains (for the ant) one more colour.'

"At the base of this reasoning, erroneous but generally admitted in comparative biology, will be found another error which is just as fundamental, and consists in admitting that, at least in the case of man, visual movements or motor reactions to light are provoked either by the sensations of light themselves, or by other psychic states (psychic representation, pleasure, displeasure, will, etc.), which, according to the psychologists, are derivatives of sensations." [1]

It seems to me, for the following reasons, that this criticism is purely verbal. The fact that we have no objective knowledge of any sensations in animals has long been a commonplace of educated men. Nuel has no justification in supposing that the authors he criticises are not familiar with this platitude. Being men, however, and writing for men, they use the language of human beings. To say that an ant "prefers" red to violet light is a short way of saying that its motor reactions under the two conditions are such that, were it endowed with a consciousness similar to that of the speaker, such a preference could be inferred to exist. If any one asserts that the ant does as a matter of fact possess a consciousness

[1] Nuel, *op. cit.*, pp. 11–12. Beer (*op. cit.*, p. 34) writes, somewhat more cautiously: "We have no right and no necessity to attribute to lower animals with no demonstrable associative memory sensations at all, and what is built up on sensations, pleasure, Unlust, Common Sensation, etc. They may have these or not; provisionally we do not require for a functional knowledge of their activities to regard them psychologically otherwise than as to us a new kind of apparatus."

similar to that of man, and twists his experimental results to agree with such a dogma, he is no doubt acting unscientifically, but I see no evidence of this in any of the numerous passages singled out by Nuel for attack. Indeed, the war might well be carried into the enemy's country. While ostensibly employing a terminology which is non-committal as to psychic states, Nuel, Beer, and others of their school often make merry at the expense of those who, however vaguely, attribute consciousness to "lower" animals. Now the one animal about the conscious states of which I "know" anything is myself; therefore when I have to consider any living creature, the structure and reactions to stimuli of which compel me to classify it with myself somewhere in the animal kingdom, I must, in default of evidence which, by definition, I cannot obtain, attribute to it some degree of "consciousness" or "blunt Occam's razor." When we turn to the inorganic world, or even to the vegetable kingdom, the physiological points of difference outweigh the points of resemblance, and the attribution of consciousness ceases to be justifiable. The suggestion of Beer and Nuel, that the conventional method of writing about the sense of animals is akin to the pre-Galilean physics which spoke of water seeking its level and nature abhorring a vacuum, is, I think, purely *ad captandum*. I admit that anthropomorphic language has sometimes led writers to go beyond their evidence, and that Beer and his colleagues have done good service in pointing this out, but I cannot think that the evil is as great as they assert, or that the remedy they propose is really an efficient one. As a matter of fact, the very authors who are particularly scornful of others' anthropomorphism not infrequently commit the same fault themselves. For instance, Professor Nuel writes: "The insect which orientates itself in flying among small obstacles reveals a remarkable development of its moto-reactions, but no true icon-reactions. To judge by what occurs in man, the latter even appear to be impossible during so rapid a movement." [1]

Why, on Professor Nuel's principles, *should* we "judge by

[1] Nuel, *op. cit.*, p. 91.

what occurs in man"? Further on he writes: "Of what nature is this visual memory of places in the hymenoptera? There is certainly no question of a revival of previous icono-reactions, of which bees are certainly deprived, and which, besides, could not be produced during so rapid a translation as the flight of a hymenopteron."[1]

The man who writes such sentences as these ought, I think, to be a little careful how he accuses others of anthropocentric errors. I shall therefore, in the brief notes which follow, make no attempt to avoid the common descriptive words used by Forel, Wassmann, and other comparative biologists.

Our knowledge of the anatomy and histology of the eyes of Invertebrata apart from Insecta owes much to the work of Hesse, ably summarised by Beer in the memoir already referred to. Exner has studied the faceted eye of insects in great detail, while the development of histological technique, particularly the silver methods of Golgi and the work of Ramon y Cajal, has enabled anatomists to describe the structure of the eyes of most vertebrata with remarkable precision.

In some quite simple animals, simple, that is, from the point of view at which we have so far arrived, the light-perceiving structures are decidedly complex; indeed the complexity of the latter by no means goes hand in hand with the general complexity of the organism, so that no satisfactory zoological classification is possible. Generally speaking, we find one or more elongated structures formed from cytoplasm or excreted by it, often exhibiting a laminated structure, and, in the majority of cases, associated with pigment. Pigment, however, is not invariably present, as, for instance, in the case of the "photirzellen" of several annelid worms and the more complex photirzellen of the leech (Fig. 7). A stage beyond the "photirzellen" is seen in the ocelli of leeches (Fig. 8), while yet more specialised are the ocelli of flat worms (Fig. 9). Some of the polychætes exhibit true camera eyes (Fig. 10), and in cephalopods the retinal structure is highly complex.

[1] Nuel, *op. cit.*, p. 104.

In arthropods we meet with a specialised type of eye, the form of which may be studied in the cockroach (*Periplaneta orientalis*). The outer surface shows many divisions, and a vertical section through the principal axis proves that the superficial divisions mark the bases of long truncated cones, the ends of which rest on a semicircular basement membrane. Each cone is a single unit (or *ommatidium*) of the eye, consisting of numerous parts, for an account of which reference must be made to works on comparative histology.

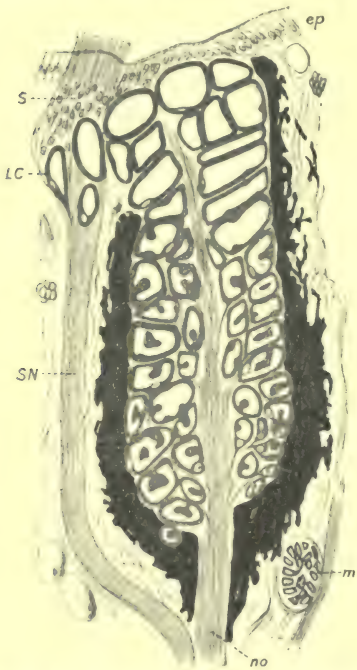


FIG. 7.—Section through an Ocellus of *Hirudo medicinalis* (Beer).

ep Epithelium. *LC* Light-receiving Cell.
S Sensory Bulbs. *no* Optic Nerve.
SN Nerve to Bulbs. *m* Muscle.

Our knowledge of the physiology of ocelli and "photirzellen"[1] is so incomplete, that we must content ourselves with saying that they are concerned in some way with the reception of luminous stimuli; with respect to the compound eyes of insects, we know a little more. The work of Exner, Grenacher, and Oscar Schmidt has demonstrated that a separate image cannot be formed on each retinular element, and that the older theory of Johannes Müller is more plausible. According to this theory, each facet will receive rays from a different part of the object, owing to the small size and great number of the facets, and as a result of the co-operation of all the facets a sort of mosaic pattern will be produced on the retina, not an immense number of small distinct images. Exner seems to have proved that the transparent structures cannot project an image, but only concentrate the rays which form the visual field of each facet. Evidently, if this theory

[1] Which may be translated by "Light-receiving Cell."

be correct, the distinctness of vision, or, to speak more accurately, the localisation of the source of the different rays, depends on the co-ordination of the facets; the greater the number of facets, the more accurate will be the localisation in eyes of the same total volume, since each facet will be smaller and illuminated by a smaller portion of the object. The advantage of having numerous small facets will be increased if the whole eye is markedly convex, because in that event not only will the visual field be increased, but fewer facets will receive rays from the same external point. We should further expect, if the theory of mosaic vision be

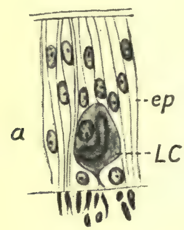


FIG. 8.

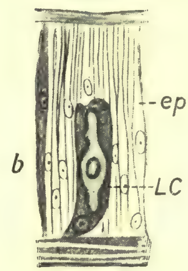


FIG. 9.

a Light-receiving Organ of *Lumbricus castaneus* (Beer).

LC Light-receiving Cell.
ep Ordinary Epithelial Cell.

b Light-receiving Organ of *Lumbricus rubellus* (Beer).

LC Light-receiving Cell.
ep Ordinary Epithelial Cell.

sound, that visual acuity, in the human sense of being able to distinguish accurately the forms of objects, would be poor in insects, while the perception of a movement should be good. All these statements are supported by the experiments of Forel. In support of the assertion that insects perceive movement better than form may be cited his observations on wasps. Forel noticed that a wasp hunting flies was frequently deceived by a nail in the wall about the same size and shape as a fly, pouncing on it more than once. When dead flies or spiders of about the same size were placed on a table the wasp carried them off indifferently, but took no notice of insects

much larger or much smaller than the dead flies mixed with them. Forel also adduces, in favour of the view that the more facets the more distinct the vision, the great visual powers of the dragon-fly as compared with the much less endowed ant. Forel has also proved by varnishing the eyes that humble-bees, wasps, and numerous dipterous insects are unable when thus blinded to direct their flight satisfactorily, while this power remains if both antennæ and the forepart of the pharynx are removed.

The numerous experiments of Lord Avebury and Forel have made it probable that bees and wasps can distinguish certain colours, and the objections of Plateau to their results do not seem to be well founded, but I have no space to give the detailed evidence. There is also reason to think that some power of distinguishing the form of objects is possessed by these insects. Forel carried out numerous experiments on a wasp, of which the following may be quoted:—

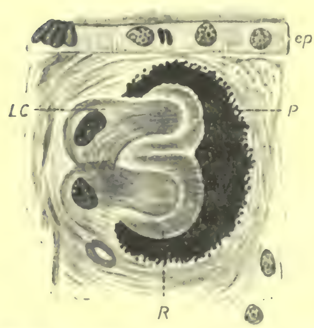


FIG. 10.—Section through an Ocellus of *Planaria torva* (Beer).
ep Epithelium.
LC Light-receiving Cell.
P Pigment.
R Roll-like Structures.

"The following day my wasp returned twice following to eat at the cross left at the same place. I then took her and removed both antennæ. She flew away, but returned half-an-hour later to eat, always at the cross, which I had left in the same place. After her departure I put a similar cross at the side of the first cross, but without honey, then on the other side a narrow band with honey, finally removing the honey cross. The wasp returned, flew straight on to the cross, alighting just in the centre (where the honey was on the other cross), and searched it vainly for a considerable time. Then, although deprived of antennæ, she began to search, doubtless recollecting that the white papers on which the honey was had already often changed in place and aspect.

"She quickly found it on the narrow band, not without,

however, having passed within a few millimetres of it two or three times without noticing it, which would not have happened to her if she had had her antennæ. She only noticed it when her mouth touched it."[1]

The great difficulty of such experiments as these is that of eliminating all disturbing factors, and the reader who desires to form definite conclusions will be compelled not only to study the works of these observers, but to perform experiments on his own account, otherwise he will be in danger of neglected sources of error which are not usually described in experimental records.

It is unnecessary to refer to the experiments which have been made on the vision of vertebrata; in general terms, it may be said that the perception of movement can be more easily shown to exist than the kind of vision associated with stimulation of the fovea centralis retinæ in man. This is, perhaps, true even for animals, such as the monkey, which possess a retinal fovea histologically similar to that of man, although in the monkey many fine movements seem to prove the existence of a type of vision altogether comparable with that of man. Of course any one who has played with a dog does not need to be told that the friend of man is far more keenly interested by moving than by stationary objects.

It will be clear that many important problems in connection with the comparative physiology of vision still await solution, and that the subject is one of peculiar interest.

BOOKS AND PAPERS RECOMMENDED FOR FURTHER STUDY

The student should first read the account of the histology of visual tissues in Principles of Animal Histology by *U. Dahlgren and W. A. Kepner*, Macmillan, 1908, then the works mentioned in this chapter in the following order: (1) Beer's paper, (2) Nuel's book (first part), (3) Forel. Ample references to the vast literature of the subject will be found in these sources.

---

[1] Forel, *The Senses of Insects*, Yearsley's translation, London, Methuen, pp. 27–28.

CHAPTER XI

RETINAL PROCESSES, ELECTRICAL, PHOTOTROPIC, AND CHEMICAL RESPONSES

THE physiology of the eye falls naturally into two main divisions: in the first we regard the organ as an optical instrument, investigate its structure, and determine the constants of the lens system together with the latter's defects and compensations. We also investigate the relations subsisting between the optical mechanism and the afferent or efferent nervous paths, together with the manner in which these relations may be modified or destroyed. This branch does not fall within the scope of a treatise such as the present. I assume the reader to possess some knowledge of the easier parts of physiological optics, and intend to deal solely with the other division of our subject. This investigation starts with the arrival of a stimulus at the retina, examines the resulting changes in this structure, and attempts to associate them with the materials yielded by an analysis of visual sensations and stimuli. In order that we may not lose sight of the wood for the trees, it is necessary to distinguish carefully between the probable and the possible, under a penalty of losing ourselves in a maze of pure speculation. When a beam of light falls on the retina, certain marked physical changes occur; in some of these cases a distinction is possible, because the reaction does not appear to be the same over the whole surface of the retina, a fact which apparently depends on the non-uniformity of structure displayed by this membrane. This statement cannot be generalised, because certain forms of response are such that we can, under possible experimental conditions, only consider their relation to the retina as a whole; an example is the photo-electric response. If the retina and optic nerve be connected up through a galvanometer, a "current of rest" is

observed, its direction depending on whether the inner or outer surface of the retina is used. When light falls on the retina, this current undergoes a somewhat complex variation. In the isolated retina there is first a positive then a negative variation; on cutting off the light a positive variation is produced. In conditions most like the normal state the positive phase is better marked in the case of the frog, but in birds and mammals a negative phase alone is obtained. This result appears in the absence of the visual purple, although the reaction is more intense if this pigment be present, and it is clear that the whole effect varies in intensity with the part of the spectrum employed.

Another general change of state is the fact that after exposure to light the retina is less readily stained with acid dyes, but this is not so definite nor so generally accepted as the electrical response.[1] Thirdly, we have the well-known phototropic reaction of the pigment epithelium. In a frog's eye which has been kept in the dark the pigment layer is easily separated from the rods and cones; the pigment granules are in the cell bodies round the outer limbs of the rods. After exposure to light, the layers can only be separated with difficulty; the pigment is much more abundant between the outer limbs of the rods, and also passes between the inner limbs as far as the external limiting membrane. This change can be induced in the frog by ten minutes' exposure to light. The various parts of the spectrum are not equally efficient in producing this change, the long waved lights, especially red, being but feebly active. The pigment will not move if the central nervous system is destroyed, and the reaction may take place in one eye as a consequence of light falling on the opposite retina. A third response is cone shortening, which appears to be due to contraction of the inner limbs. Just as in the last case, cerebral injury abolishes the power of movement, and the change may be produced indirectly by stimulation of the opposite eye. Here, again, the various spectral lights differ in power to stimulate, but certain peculiarities may be noticed. Red light produces a

[1] See Dittler, *Pflüg. Arch.*, 1907, cxx. 44.

greater effect than on the pigment cells, and shortening may follow stimuli other than light, *e.g.* changes of temperature. Cone shortening also seems to take place in mammalian eyes, while the pigment change is only definitely established for the frog.

Finally we come to the important question of Visual Purple or Retinal Red. This is a substance of a deep purple-red hue, present mainly (*perhaps* entirely) in the outer limbs of the rods. On exposure to light the pigment is rapidly bleached without passing through an intermediate yellow stage, as has frequently been asserted. This bleaching is limited to the part upon which light falls, and the latter is alone capable of decolourising the pigment in a living eye. Regeneration takes place either in darkness or red light, apparently depending on the existence in or production by the pigment epithelium of a substance called by Kühne Rhodophyllin, as suggested by the following experiment. When a frog is curarised, œdema occurs between retina and choroid, and the former is separated from the pigment layer, which tends to adhere to the choroid. If the frog be now exposed to light until bleaching results, no regeneration occurs on detaching the retina and placing it in a dark chamber; but if the pigment layer is simply placed in contact with the retina, new formation proceeds as under normal conditions. We seem, therefore, entitled to assume that regeneration is independent of direct continuity, and is due to chemical or physical processes. It was once believed that the formative substance is derived from the coloured globules in the epithelial cells, but this is probably incorrect, as the process seems to occur when they are wholly or mainly absent, as in the albino rabbit. Visual purple can be extracted from the retina with a solution of bile salts, and its absorption spectrum has been examined; the absorption does not appear to be identical in purple from different animals, but the significance of the variations is unknown.

If we compare the bleaching powers of the homogeneous lights, we find that red and yellow are practically inoperative, the parts of the spectrum falling between the Fraunhofer D and E lines having, on the other hand, maximal powers.

If we ask ourselves what value these facts have for a study of visual processes, we shall conclude that some distinctions must be made. In the first place, experimental conditions requisite for observing electrical changes render the co-ordination of the latter with sensation-differences hardly practicable. Haas suggested that the electromotive response could be regarded as a measure of sensation-intensity, and plotted the curve obtained when the light intensities were taken along one co-ordinate axis and the electromotive response along the other. If the stimuli were increased in geometric and the electromotive responses varied in arithmetic ratios, as they should if Fechner's law holds, the curve would be a straight line. Haas' figure shows that this is only very roughly true, and in any case the assumption that the electromotive response is a measure of sensation-change appears to be quite arbitrary. Perhaps all we can safely infer is that light produces some change of state in the retinal structure, a change not of the same magnitude, nor even, it may be, qualitatively identical when we employ stimuli of different wave lengths; the exact relationship between physical process and psycho-physiological response is still obscure. These remarks also apply to the phototropic movement of the pigmented epithelium and the shortening of the retinal cones, but on turning to the facts relating to visual purple, we are tempted to pursue our investigation further. Here we have a substance only, or at least mainly, present in certain areas of the retina; if it play a part in the physiological processes of vision, these should be different in different regions. We might, of course, have the final result, the visual sensation, identically the same even if the physiological precursors were quite different; but if, in fact, we find that visual sensations yielded by stimuli acting on different parts of the sensitive area are not uniform, that a modifying factor applied to the whole retina affects it differentially, we have some ground for attributing definite importance to the visual purple. To obtain the grounds necessary for forming a judgment on this point, we must first ascertain what alterations in visual responsiveness are produced by changing the totality of conditions to which the

eye is subjected; secondly, we must know whether the changes are entirely or chiefly confined to any particular region; and lastly, whether any structural peculiarities give us a plausible explanation.

It has long been known that the nature of the response of the eye to a stimulus largely depends upon whether, before the experiment, the subject has rested in a dark room or been exposed to light, that is to say, whether there is a condition of light or dark adaptation. The detailed study of these and allied phenomena will form the subject of the next two chapters.

RECOMMENDED FOR FURTHER STUDY

W. Nagel, Die Wirkungen des Lichtes auf die Netzhaut (Nagel's Handbuch der Physiol., Bd. iii. pp. 91–108) contains an excellent account, with full references to the literature.

CHAPTER XII

VISUAL ADAPTATION—PERIPHERAL VISION TOTAL COLOUR-BLINDNESS

As was mentioned at the end of the last chapter, the fact that different parts of the retina are unequally responsive to light has long been known, and the path which led up to this knowledge was a study of the facts of visual adaptation to varying intensities of light.

Aubert was one of the first exact observers to notice that the response of the eye to feeble stimulation was heightened by a sojourn in darkness. He also noticed that the threshold value of a stimulus in such cases varied inversely as the area stimulated. Since this could only mean that when light fell on the peripheral part of the retina its value as a stimulus was enhanced, Aubert's observation really contained the nucleus of all subsequent work. His general results were speedily confirmed. Charpentier, among others, found that the central part of the "dark" retina, although exhibiting an increased responsiveness as compared with the same region in the "light" eye,[1] was much less responsive than the periphery. This increase was more marked in the case of the short waved spectral colours, and there is even some doubt whether adaptation makes any difference at all to the activity of red rays. It is also rather uncertain whether the fovea centralis retinæ is affected by resting in a dark room; the evidence is conflicting, and the matter is still too controversial for it to be discussed here.

A particular case of adaptation which is of much interest is "Purkinje's Phenomenon," an effect which can be described in the following way. If one examines an ordinary spectrum, the brightest part of it seems to occupy the neighbourhood

[1] I shall speak of an eye which has been rested in the dark as a "dark" and one previously exposed to light as a "light" eye.

of the yellow or orange-yellow; if, however, the physical intensity of the spectrum be diminished, for instance, by moving the source of light farther away from the prism, the maximum of apparent brightness shifts towards the violet end. With the feeblest illumination which enables one to distinguish the spectral colours at all, the brightest part is at the junction of the green and blue. Ewald Hering has, in my opinion, demonstrated that these changes are due to adaptation, using an experimental method of characteristic simplicity and elegance. Two rooms which could be independently darkened are separated by a light-proof partition, in which two slits are cut and covered with pigmented glass. The amount of light transmitted by these slits could be varied independently with the aid of reflectors. So long as the room occupied by the observer is kept at a constant illumination, diminishing the physical intensity of the light traversing the two slits, which are covered with blue and red glass respectively, does not change their relative intensities. If, however, the observation room is darkened, the blue slit immediately appears brighter than the red one, even while the physical intensity of the light passing through them is unaltered. The effect is much enhanced by a stay in darkness, and is more noticeable in indirect (peripheral) than in direct (foveal or central) vision. Burch has noticed a similar phenomenon, and we may fairly consider Purkinje's effect as dependent not on physical intensity, but adaptation.

Before going further, we must ask ourselves one question, What does one mean by saying that different colours are equally or unequally bright? I am not acquainted with any really complete answer, and shall fall back upon a purely empirical justification. Ask a dozen normal persons to look at a spectrum in daylight, and one finds they all agree in picking out some part of the orange-yellow, which they call the brightest point of the spectrum. They mean, I take it, that this part produces somehow a predominant effect in consciousness. How this comes about is matter for a psychological discussion; it is no part of the pure physiology of vision. If we adopt this relatively humble standard of brightness, comparative results are attainable in numerous

ways. One of the best methods is that of "flicker," to which Haycraft and Rivers have devoted much attention. When a series of sectors are whirled round on a machine called a colour mixer, the velocity necessary to produce a fused sensation depends upon the brightness of the sectors; hence with different sets of sectors equal in size, the velocity of rotation which just extinguishes the sensation of flicker affords a measure of brightness, which may be taken, within fairly wide limits, to vary inversely as the rapidity of rotation. It may be well to remark here that work of this kind, like most researches on the sense of sight, is easy neither to perform nor to interpret. To carry out satisfactory experiments on a single person requires much attention to details, and even when the obstacles have been surmounted we have to consider the question of individual variations. The problem of variations in the reaction to sensory stimuli is just as urgently in need of adequate statistical treatment in the case of sense physiology as in any other biological field, and even less likely to obtain it.

Hering several years ago noted the relative darkening of red as one passes from central to peripheral vision; he compared a pure red, a spectral mixture of red and blue-green (656 $\mu\mu$ + 470 $\mu\mu$), and daylight. The converse was found to hold for spectral green (505 $\mu\mu$), but his results were not quite satisfactory, for momentary dark adaptation occurred during the experiments. Tschermak, who studied the whole question systematically in the "light" eye, found in indirect vision a relative diminution in brightness for light of wave length between 693 and 525 $\mu\mu$, no change from 525 to 516 $\mu\mu$, an increase from 516 to 466 $\mu\mu$. Similar changes were observable in "dark" eyes.

Another method was to start with a large field of colourless light, produced by mixing together complementaries, and then to diminish its size. It has been found that a colourless mixture of spectral red and bluish-green becomes, with such a real diminution, redder and darker; if the change of size be an increase, it becomes greener and brighter. In fact, both for "light" and "dark" eyes colourless matches valid for the periphery do not hold for the fovea centralis,

and *vice versa*. Apart from adaptation, it is interesting to see whether merely changing the intensities (physical) of two mixtures renders the match invalid. On this point much difference of opinion exists, which is not surprising in view of the experimental difficulties which have to be encountered. One subsidiary phenomenon which was studied in this connection deserves a word of description, but the main question is too complicated and too controversial to be worth following up.[1] In studying Purkinje's phenomenon, we found that if the intensity of a spectrum were diminished a point was reached at which the brightest part appeared to have been shifted towards the violet. What, it may be asked, happens if the illumination be still further diminished? Under normal circumstances we soon reach a point at which the whole spectrum appears colourless, differing however in brightness in the various parts. Reduction beyond this yields an intensity which is associated with no sensation at all. Hence it seemed necessary to distinguish between the absolute liminal intensity of a spectrum, that is, the least intensity corresponding to a colourless sensation, and the "specific" threshold value for which the spectral zones could be seen to differ in hue. In determining these absolute and specific thresholds, great divergences were found between the results of different workers. The observations of Burch go far to prove that the existence of a specific threshold, at any rate in the case of foveal or direct vision, depends upon the after-effects of previous stimulation. This physiologist first performed some qualitative experiments which are most suggestive. A Bunsen burner was completely covered by a metal chimney, so as to prevent any escape of light while not interfering with ventilation. By bringing the flame into contact with the metal chimney the latter could be heated gradually to a point at which it became luminous. If the experiment were performed in a room with windows covered by ordinary blinds—that is to say, in a room from which light had not been absolutely excluded—the first appearance of light

[1] Further information will be found in the article by the present writer contributed to *Further Advances in Physiology*, London, 1909 (Arnold), pp. 354, etc.

Adaptation Values (*Burch*).

A. During the period of increasing adaptation.

Time in Dark. (Mins.)	Intensity of Minimum Visible Red.	Intensity of Minimum Visible Blue-Violet.	Ratio, V : R.
9	16·63	254·76	15·32
21	11·14	57·61	5·17
60	2·4	5·39	2·24

B. After spending two hours in the dark room.

Time in Dark. (Mins.)	Intensity of Minimum Visible Red.	Intensity of Minimum Visible Blue-Violet.	Ratio, V : R.
120	1·0	1·0	1·0
122	1·20	1·63	1·34
125	2·69	5·14	1·91
127	5·04	12·44	2·47
130	50·02	225·72	4·51

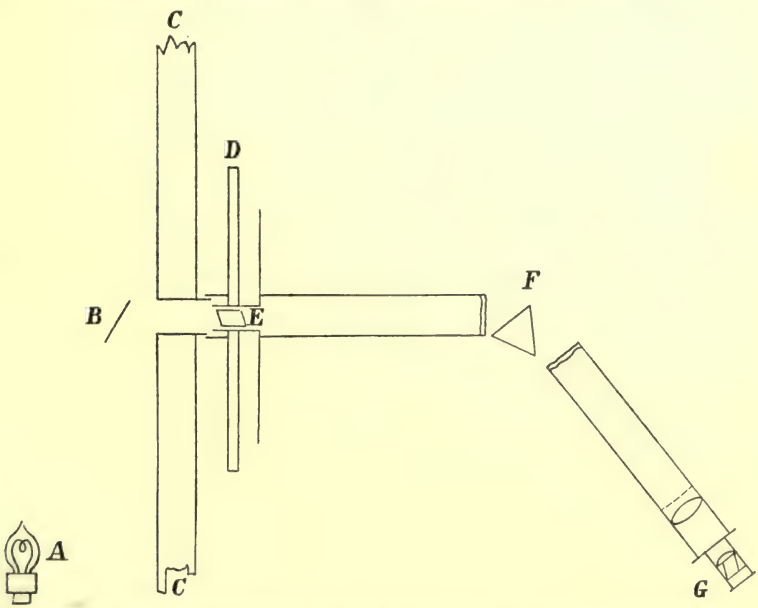


FIG. 11.—Burch's apparatus for the study of "achromatic thresholds."

A. An electric lamp, 16 candle-power. *B*. Paper reflector.
CC. Wall of dark room. *D*. Stand with polarising prism (*E*).
F. Spectroscope with double image prism (*G*) over eye-piece.

There is a stop with two slits (allowing red and blue-violet light to pass through) in the eye-piece. By rotation of the polarising prism the relative intensities of the red and blue-violet lights can be varied.

A. *Relative Stimulus Values of different Spectral Regions* (*Parinaud*).

Fraunhofer Lines.	Adapted Retina.	Unadapted Retina.
B	$\frac{1}{400}$	$\frac{1}{400}$
C	$\frac{1}{100}$	$\frac{1}{100}$
D	$\frac{1}{10}$	$\frac{1}{80}$
E	1	$\frac{1}{100}$
F	1	$\frac{1}{500}$
G	$\frac{1}{100}$	$\frac{1}{1500}$
H	$\frac{1}{250}$	?

B. *Increased Responsiveness of Peripheral Retina* (*Dark-adapted*). Stimulus: A bluish-white object, 35 degrees in diameter (v. Kries, p. 171).[1]

Responsiveness (Arbitrary Scale).	Temporal Eccentricity in Degrees.	Nasal Eccentricity in Degrees.	Insensitive Zone.
1·0	1·07	0·85	1·92
1·78	1·22	1·06	2·28
7·12	1·70	1·38	3·08
16·02	2·3	1·92	4·22
28·48	3·0	2·58	5·58
44·50	3·75	3·33	7·08
64·08	4·04	4·04	8·08

[1] Distances from the fovea centralis of any point on the retina can be conveniently measured in terms of the angle subtended at the nodal point by a segment of the retina cut by a plane passing through the fovea, nodal point,

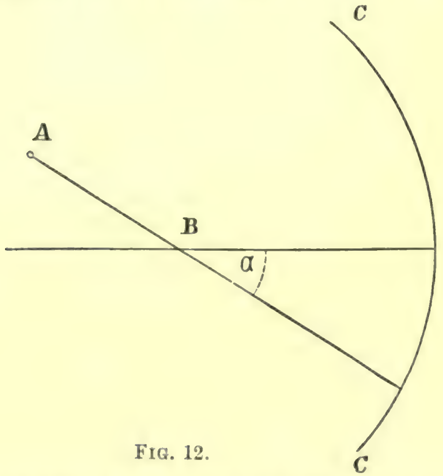


FIG. 12.

and position of the object, and bounded by a straight line through the nodal point from the object intersecting the retinal segment and by the principal axis. *E.g.* if A be an object, B the nodal point, and CC a section of the retina, the position (eccentricity) of the image of the point A is defined by the angle *a*.

was a pearl-grey tint, the achromatic threshold which others had noticed. But when the room was changed to one without windows and absolutely dark, the first appearance of luminosity was not grey, but dull red. On repeating this experiment, *after spending a few minutes in a lighted room*, the former grey appearance was once more obtained. Quantitative experiments were then performed with the apparatus shown in the diagram on page 105.

Burch was also able to show that a form of after-images (his "dazzle tints") are very persistent, and may endure as long as two and a half hours after exposing the eye to light, so that his contention can almost be regarded as established in the case of direct vision. That an absolute as distinct from a specific threshold exists in the case of peripheral vision seems, on the whole, probable in view of the careful work of Armin Tschermak, who used very prolonged dark adaptation; but Burch's work is quite sufficient to show how cautious one must be in interpreting results obtained by these methods, and how complex they are.

Direct experiment, therefore, seems to have established the following points:—

(1) The peripheral regions of the retina are relatively more sensitive than the fovea to light of moderate or short wave length.

(2) Adaptation to darkness is characterised by an increase in responsiveness to short-waved light, and this change is mainly, if not entirely, extra-foveal.

The tables illustrate these statements. The intensity values are arbitrary, the measurement of eccentricity is in terms of the angle subtended at the nodal point of the eye.

We now come to indirect evidence tending in the same direction; of this the facts relating to total colour-blindness are the most striking.

Total colour-blindness is almost always a congenital defect, and is characterised, apparently, by a complete absence of colour perception in the ordinary sense; it differs *toto cælo* from the condition of partial colour-blindness, which will be described in a later chapter. A person in this state may see a spectrum merely as a grey strip unequally bright in the

different parts which seem to us of distinct hues. To describe the sensations of a second human being must be impossible, but perhaps we may say, for the sake of comparison, and without pretending to real exactness, that a totally colour-blind man receives from a coloured print impressions similar to those excited in ourselves by an uncoloured one. A summary of the observations of Hering on a typical case will give the reader a better idea of the facts than any catalogue of signs and symptoms.

Hering's Case of Total Colour-blindness.

Coloured Circle.	Equally Bright Circle for Colour-blind.		White Valency.[1]	White Valency of a Grey Circle matching the Coloured Circle for a Normal "Light" Eye.
	White.	Black.		
	Degrees.	Degrees.	Degrees.	Degrees.
Bluish-red . .	13·0	347·0	18·8	40
Yellowish-red .	5·5	354·5	11·4	46
Orange . .	37·0	323·0	43·4	159
Yellow . .	136·5	223·5	140·2	283
Arsenic-green .	228·0	132·0	230·5	205
Green . . .	152·0	208·0	155·5	137
Greenish-blue .	109·5	250·5	113·7	89
Ultramarine-blue	88·3	271·7	92·8	34
Violet . . .	47·5	312·5	52·7	32

The subject was a man of twenty years, whose colour vision had always been abnormal. He said that he could read without difficulty, provided the light were not too intense, but that his eyes were readily fatigued by bright illumination. In twilight his vision was especially good, particularly if the light were very feeble. On examination, the following results were obtained. No objective changes were detected with the ophthalmoscope, nor was any part of the retina insensitive; there was no totally blind area (or scotoma). His power of distinguishing two spots unequally bright—physically—was much below that of a normal person, in

[1] For methods of measuring white "valency" consult Hering, pp. 567, etc. For the present purpose the figures in the third column of the table may be regarded as a recalculation of the amounts of white in the sectors which match the coloured circles, so as to admit of comparison with the figures of the fourth column.

bright light; in a dark room, it was much superior. With a spectrum, it was found that the area of red which produced any sensation was much diminished; there was shortening of the red end, and those parts which were effective seemed less bright than to a normal eye. The violet end, on the other hand, was not shortened, and it seemed relatively brighter than to the normal "light" eye, while the region of maximal brightness was in the neighbourhood of Fraunhofer's E and C lines. Brightness matches between coloured sectors and mixtures of black and white gave the results indicated in the table, which contains comparative values for the normal "light" eye. It is to be noted that the colour-blind's matches were valid, *i.e.* good matches, for a normal "dark" eye.

Tests were also carried out polariscopically. At one end of a horizontal tube, blackened on the inside, a cork plate was fixed; the plate was perforated in the middle and a doubly refracting prism inserted. The other end of the tube was closed by a lid, in which two equal and symmetrically placed semicircular openings were made. With this contrivance the ordinary and extraordinary images obtained by polarisation appeared to form a series of circles when the tube was directed to a source of light, *e.g.* a piece of baryta paper stretched over a glass plate. Between the eye and the prism a small telescope and a Nicol prism were introduced, together with a graduated arc. The diaphragm of the telescope removed the lateral images, leaving only two magnified white circles, the halves of which could have their brightness altered in opposite directions by rotating the Nicol prism. In front of one opening in the tube a coloured glass was placed, and the Nicol so arranged that for the normal "dark" eye or for the totally colour-blind eye, both halves appeared equally bright. The next table gives the readings for two observers. Some of the variations may be explained by the fact that the normal-sighted person was unpractised in this sort of work.

Precisely similar results were obtained in matching spectral colours.

The analogy between normal vision under conditions of

Polariscopic Matches (Hering).

Yellow Glass.		Blue Glass.	
Total Colour-blind.	Normal Dark-adapted Eye.	Total Colour-blind.	Normal Dark-adapted Eye.
Degrees of Rotation.	Degrees of Rotation.	Degrees of Rotation.	Degrees of Rotation.
22·3	22·9	18·2	18·35
22·6	22·6	18·0	17·95
22·3	23·0	18·0	18·15
21·9	22·5	18·1	18·4
22·3	22·7	17·8	18·9
21·8	23·1		
22·1	21·8		

dark adaptation and the vision of the totally colour-blind will also be apparent from the next two tables. The first gives the intensity values of the different parts of the spectrum for a normal "dark" eye, and the second Abney's observations on two other cases of total colour-blindness. The units of intensity in these tables are not comparable, but it will be observed that the maxima occur in the same part of the spectrum.

"Twilight" Values of a Spectrum (Schaternikoff).

Wave Length.	Intensity Value.	Wave Length.	Intensity Value.
In millionths of a mm.		In millionths of a mm.	
670·8	18·0	529·3	2736·0
651·8	36·5	522·3	2532·3
634·3	83·3	515·4	2219·3
618·1	216·9	508·7	1944·0
603·1	423·2	502·2	1475·8
589·3	881·7	490·0	1016·0
577·1	1424·9	478·6	633·0
566·4	2110·7	468·0	364·5
556·0	2609·7	458·7	208·8
546·0	2899·0	451·1	111·2
537·2	3000·0	443·9	69·6

Since the direct evidence which we studied first suggested that adaptation was an affair of the extra foveal part of the retina, one might expect the fovea centralis in the totally colour-blind to be relatively insensitive. As a matter of fact, in seven out of eighteen cases which have been investigated, an absolute or relative central or para-central scotoma was

observed, and in most cases very imperfect fixation or even nystagmus was noticed. It may, however, be regarded as certain that the existence of such an insensitive area is not necessarily found in typical total colour-blindness; as we shall see later, the point has been laboured chiefly for theoretical reasons.

Luminosity Values of two Cases of Total Colour-blindness (*Abney*).
(No. 40 in Abney's scale is close to the E line.)

Scale of Spectrum.	K. B.'s Luminosity Value.	P.'s Luminosity Value.
56	2·5	...
54	9·0	...
52	16·0	7·0
50	27·5	19·0
48	42·5	39·0
46	61·0	65·0
44	82·5	85·0
42	96·0	98·0
40	100·0	99·0
38	95·5	91·5
36	87·5	90·0
34	75·0	80·0
32	61·5	65·0
30	43·0	50·0
28	37·0	36·0
26	30·0	26·5
24	24·0	19·5
22	18·5	14·0
20	14·5	10·0
18	11·5	...
16	9·0	5·5
14	7·0	...
12	5·0	...

In general terms, we may say that the analogy between normal vision under conditions of dark adaptation and the vision of the totally colour-blind is quite close. In the next chapter some additional evidence will be considered, and the theory of the matter discussed.

RECOMMENDED FOR FURTHER STUDY

Sufficient indications to enable the reader to consult original sources of information will be found in the article Visual Adaptation, by *M. Greenwood*, Further Advances in Physiology, London, 1909 (Arnold), pp. 351–377. Of the literature there referred to, the memoir by Tschermak is the most exhaustive.

CHAPTER XIII

RECURRENT VISION-THEORIES OF ADAPTATION

A SET of experiments of apparently little importance has thrown considerable light on the question of adaptation. These deal with the effects which follow the application of luminous stimuli for very short intervals of time.

Such experiments can be carried out in at least two ways. By a contrivance similar to the shutter of a camera the eye can be stimulated for a very short time, or, the gaze being fixed, a source of light may be moved across the field of vision. In the latter method, a disc with a slit in it can be rotated in front of a lantern. If the length of the slit is l, and v is the velocity of movement, l/v measures the time during which each retinal element is exposed to the light, and we can make this time as short as we please. There is of course no difference in principle between the two methods, but the second is rather easier to employ, and the results obtained with it are of special interest.

If a bright object is rotated in this manner on a screen with a slit in front of a light, the whole sensory effect comprises the following phases :—

(1) A primary image; the immediate consequence of the stimulus, also its strongest effect. As compared with the image due to a stationary illuminant, it is more or less elongated into a streak of light.

(2) Immediately following upon the primary image is a short, dark streak.

(3) After the dark streak comes a second period of illumination which, if the stimulus be coloured, appears tinged with the complementary. In a successful experiment this effect may be so pronounced that it seems as if a second object were following in the track of the first, so that it has

been termed the "satellite" or "ghost," and the whole phenomenon is described as that of "recurrent vision."

(4) The end of the satellite is not sharply defined, and is followed by another interval of darkness.

(5) The field once more brightens, but somewhat faintly, and an image of the same colour as the primary one appears.

(6) Lastly, another dark interval is obtained.

It would hardly be expected that there should be complete accord in the description of so complicated an effect as witnessed by different observers. Hess and v. Kries, to mention two highly trained and experienced sense physiologists, differ materially in their accounts as to what can and what cannot be seen.

The work of v. Kries has received, in all essential points, confirmation from the experiments of Macdougall, and I shall follow his description as closely as possible.

With respect to the experiment as a whole, we have three phases of illumination—the primary image, the satellite image, and the tertiary. In apparent brightness these are ranged in the order of their appearance. When the original stimulus is of low intensity, no tertiary image is obtainable; with a still less intensity, the satellite also disappears. The lengths of the images can also be made to vary, and the dark intervals to vanish. Fixing our attention on the primary, the following characters have been found. The image is sometimes striped, but apart from this is uniform when viewed under conditions of light adaptation. As dark adaptation proceeds the image not only increases in extension and brightness, but with chromatic stimuli ceases to be uniform. Thus with blue light, only the anterior border is deep blue, and is followed by a whitish stripe. Macdougall found that the white part begins at a distance corresponding in his experiments to a time interval of $\frac{1}{18}$ second. With other colours, *except red*, the same result is obtained, but less distinctly.

The satellite image begins $\frac{1}{4}$–$\frac{1}{5}$ second after the commencement of the primary, and is generally complementary to it. This rule must, however, be modified in the following way. If the primary is pure white, the secondary is bluish;

in fact, the secondary is always modified in the direction of bluishness. Even with a feeble blue primary, the secondary may still have a faint bluish tinge. As regards brightness, the result depends on the adaptive value of the stimulus, *i.e.* two lights of equal stimulus values for the "dark" eye give equally bright secondary images. Red, with its relatively low stimulus value for the "dark" eye, only gives a secondary when its physical brightness is great.

As we should expect from its character, the satellite is largely dependent on the adaptation of the eye, increasing to a maximum as dark adaptation proceeds, and then diminishing, although it persists after prolonged dark adaptation (Macdougall). We associate, therefore, with the satellite the ordinary characters of peripheral vision, (1) relatively greater efficiency of the shorter waved lights, (2) increased intensity on dark adaptation; it only remains to add failure on foveal stimulation. With respect to this failure, a somewhat heated discussion took place between v. Kries and Hess, the latter asserting that a distinct satellite could be obtained in central vision. V. Kries has, however, indicated certain possible fallacies in Hess' technique, and his assertion that no secondary can be produced at the fovea centralis has been confirmed by the work of Hamaker and of Macdougall. Passing to the tertiary image, the following characters may be noticed. The hue is best appreciated when red is chosen as the stimulus; in such a case, the tertiary may be very distinct. With increasing dark adaptation, the tertiary gains in brightness but loses in chromatic value; owing to the high adaptive values of green and blue when these lights are used at moderate intensities, the coloration of the tertiary image can only be seen at the beginning of the experiment. There is some difference of opinion as to whether this tertiary image can be seen in direct vision; since red light is the most suitable stimulus for calling it up, it should be so perceived. Perhaps there are two factors in the production of the tertiary—a chromatic element unaffected by dark adaptation, and a brightness element which is so affected.

The last group of facts to which I desire to refer in this connection are those which have to do with observations

upon the pupillary reaction. Schirmer asserted that the pupil width and its reaction were related to the adaptive condition of the eye. With complete adaptation to a given grade of light, the pupil reaches after an initial widening or narrowing a physiological mean position. Garten found that momentary illumination produced in "light" eyes a weak sudden, in the "dark" eye a slow powerful contraction. Proceeding further on these lines, Sachs discovered that the pupillo-motor response to coloured lights followed closely their adaptation values. Abelsdorff confirmed these results, using the apparatus sketched.

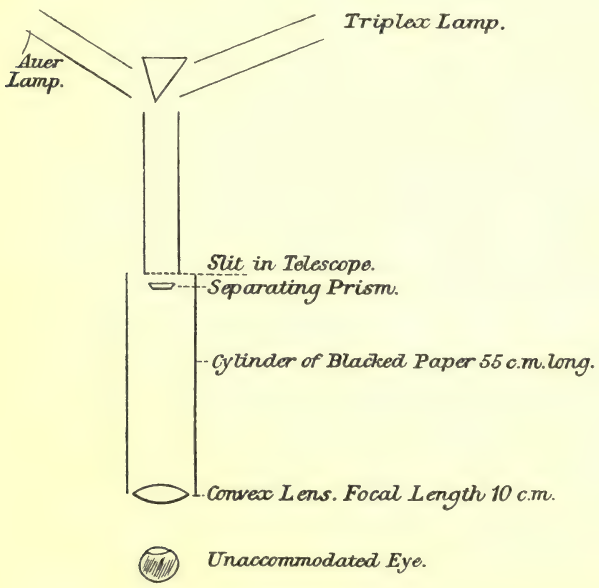


FIG. 13.—Abelsdorff's apparatus for studying the pupillo-motor response.

One of the two lights serves as a standard; the subject, looking through the strong convex lens at the slit, sees a bright point surrounded by a diffusion circle. If the light falling on the eye be changed, the diffusion circle increases or diminishes in size. By rotation of a Nicol prism the new intensity can be increased or diminished, and the intensity is found for which the diffusion circle produced by the standard

light is not increased or diminished by changing to the tested colour. This method is more accurate, in Abelsdorff's opinion, than one might suppose, the mean experimental error being about 7 per cent. The next table gives some of Abelsdorff's results:—

Pupillo-Motor Values.

Wave Length. $\mu\mu$.	Comparison Lights.		
	600 $\mu\mu$.	Light Adaptation. 480 $\mu\mu$.	Dark Adaptation. 480 $\mu\mu$.
	Mm.	Mm.	Mm.
640	·5271	·3920	·2666
620	·8523	·8376	·5670
600	·9720	·9822	·7260
580	·9536	·9090	·8065
560	·8303	·8739	·8865
540	·5518	·6141	·9200
520	·3333	·2936	·5755
500	·1181	·09141	·1612

Brightness Values.

(Readings obtained when the same subject adjusted the intensities of the lights until they seemed to be equally bright.)

Wave Length. $\mu\mu$.	Comparison Lights.		
	600 $\mu\mu$.	Light Adaptation. 480 $\mu\mu$.	Dark Adaptation. 480 $\mu\mu$.
	Mm.	Mm.	Mm.
640	·5253	·3518	·2529
620	·8204	·7230	·5515
600	·9431	·9090	·8536
580	·9431	·9090	·8535
560	·8811	·8613	·9540
540	·6259	·6354	·9540
520	·3700	·3189	·5750
500	·1168	·0944	·1612

The close agreement between the pupillo-motor values and those of apparent brightness justifies the method, and its importance lies in the fact that we can employ it in experi-

ments on animals. We have no direct means of investigating adaptive changes in any animal except man, but we can measure this pupillary response; if we find it changing in the manner described, it is suggested (not, of course, demonstrated) that in such animals the visual responsiveness may be similarly affected. It has been found that the intensities of red and blue, which appeared equally bright to, and exerted the same pupillo-motor effect upon, a human "light" eye, did not produce identical changes in the pupils of the dove and the owl. For the former the red, for the latter the blue, was the stronger stimulus. Indeed, the pupillo-motor response to blue in the owl's eye was greater than in the case of a total-colour-blind (Abelsdorff).

We can now appropriately examine the theories which have been propounded to describe these different classes of fact. In the first place, can we justly say that there is any functional difference between the spot of distinctest vision, the fovea centralis retinæ, and the paracentral or peripheral regions of the retina in respect of colour vision?

In view of the long series of experiments bearing upon the Purkinje effect, the increase in brightness of the short-waved spectral lights at the expense of the long-waved vibrations, it seems clear that this effect is mainly if not entirely peripheral. Even those who claim to have observed foveal adaptation admit it to be much less marked than peripheral changes of responsiveness. We have also seen that these adaptive changes consist in a greatly increased responsiveness to light of short wave length, such appearing more intense than under "light" conditions. We have to account theoretically for a localised change in responsiveness with respect to certain forms of stimulus.

The difference in histological structure between the fovea centralis and the surrounding area caused Schultze, many years ago, to suggest a functional separation, a conclusion which he supported by evidence drawn from the study of comparative anatomy. When Schultze wrote, however, our knowledge of adaptive changes was little advanced, and his conception went unheeded. The modern development of Schultze's hypothesis is due to the independent researches of

H. Parinaud and J. v. Kries, both of whom, together with their colleagues and pupils, have published numerous memoirs on the subject. The actual priority appears to belong to Parinaud, whose first paper was published in 1881.

Essentially the theories of Parinaud and v. Kries are exceedingly simple. Two distinct visual mechanisms exist: of these, one is concerned in the elaboration of chromatic and achromatic stimuli, and is represented in the retina by the cones; the other mechanism deals with achromatic responses only, and is represented by the rods and visual purple. The former mechanism is the only one which can act in bright light, and its responsiveness is little, if at all, increased by resting in darkness; the latter is brought into play when the eye has been shielded from stimulation, being the sole or chief agency for twilight vision; it is characterised by special responsiveness to ethereal vibrations of short wave length. In view of the double nature of the mechanisms postulated, the theory has been named the "Duplicity Theory" ("Düplizitätstheorie"). Let us see how far the hypothesis covers the experimental observations I have enumerated. If the theory were true, we should expect (1) spectral maximal brightness to change in favour of the violet end when the physical intensity of the light is diminished; (2) this change ought not, however, to occur in images formed at the fovea centralis retinæ; (3) no achromatic threshold ought to be obtained for any light at the fovea centralis or for red light anywhere.

Each of these deductions has been shown to receive support from experiment and observation.

Another way of testing the theory is to see whether we have any forms of vision in which, apparently, the basal mechanism is similar to that associated by the theory with twilight vision, and uncomplicated by any other type of vision. The subjects of total-colour-blindness appear to afford us a case in point. We found that the brightness judgment of these people agree well with those of normal men in a state of dark adaptation; that there is evidence in such cases of diminished or absent foveal responsiveness, bad fixation, inferior acuteness of vision, nystagmus and

abnormally good vision in twilight. This might well be regarded as a case in which the twilight mechanism alone is operative. Conversely, one pathological condition is consistent with the activity of the hypothetical daylight mechanism existing by itself. This is the condition of "night-blindness," or hemeralopia, as it is badly called, which has been investigated by Parinaud, Nettleship, Messmer, and others. According to Parinaud, subjects of this disease have vision of the foveal type; their colour sense is normal, but the spectrum is shortened at the violet end, and responsiveness to feeble stimuli is abnormally poor. It is the latter condition which incapacitates a person who exhibits the peculiarity to a marked degree from working in twilight or poor artificial light. The investigations of Messmer have made it seem very improbable that night-blindness is a simple condition. In some cases, dark adaptation is very slowly induced, but after a sufficiently long time attains a normal degree of intensity. In other cases, a certain degree of adaptation is produced in the normal time, but the amount is far less than in ordinary persons. Owing to the complexity of the condition, we must admit that the light it throws on our problem is not so great as we could wish. Provisionally, we may perhaps say that some cases of night-blindness can be interpreted by supposing that the hypothetical daylight mechanism is alone functioning, while most of the examples of total-colour-blindness agree with the supposition that the twilight mechanism is chiefly at work. It must be pointed out that there cannot possibly be a complete identity between the normal peripheral mechanism and the visual system of a total colour-blind. Poor as is the latter's visual acuity, it is far superior to that of the peripheral parts of the normal retina.

The complex results in sensation which are due to short or moving stimuli have perhaps confused some readers; let us see whether our hypothesis is capable of arranging them in an orderly manner. The peculiar striping of the primary image has already been mentioned, how blue tails off into white; this suggests the interplay of two processes. I also emphasised the dependence of the secondary image on

adaptation, and its probable absence at the fovea centralis. We can perhaps sum up the effects in terms of our hypothesis thus:—

The cone mechanism responds by two effects, the main part of the primary and the colour component in the tertiary. The rod apparatus responds in a threefold manner; it gives us the white tail of the primary, the whole of the secondary, and contributes, although slightly, to increasing the brightness of the tertiary. This description clears up some difficulties, but raises others. If we are to regard the twilight mechanism as solely responsible for the secondary image, it is clear that we derive sensations of colour as well as sensations of luminosity without hue from that mechanism, since the secondary image is often coloured. The mechanism cannot therefore be identical with that of a totally colour-blind eye; we must either give up the view that total colour-blindness is a condition in which the rods and purple react *as in a normal person*, or regard the secondary as due to something beyond rod stimulation. The latter alternative is the one v. Kries is disposed to adopt, but we have then the difficulty of understanding why the secondary is entirely peripheral. Are we to suppose that there is a functional difference between the central and peripheral cones? If not, why in this case can the cones only respond if the rods are at the same time stimulated?

Probably this will be found the most serious difficulty in the way of a complete acceptance of the duplicity hypothesis. It is hoped, although not expected, that further experimental work will clear the matter up.

A certain amount of confirmatory evidence has been brought forward from the side of comparative physiology. It has long been known that the relative numbers of rods and cones differ in various animals. Thus, the rods are very large and almost exclusively present in the retinæ of nocturnal animals, such as owls, bats, and hedgehogs. In many other creatures, on the other hand, including most birds, cones predominate. It was, indeed, on the strength of this that Schultze advanced a theory essentially similar to that of Parinaud and v. Kries. Kühne subsequently

showed that visual purple was present only in retinæ containing rods, although he was not able to extract the pigment from all rod-containing eyes, an exception being the bat. Trendelenburg has recently extracted visual purple from the retinæ of more than one species of bat. Experimentally, as we have seen, Abelsdorff found that, judging by the pupillo-motor response, the owl is specially sensitive to short-waved light and the dove insensitive.

We all know that most nocturnal animals can see badly in broad daylight, while such birds as the pigeon exhibit a marked degree of night-blindness. In Parinaud's words: "It is a matter of common observation that hens and pigeons see very imperfectly in artificial light, and defend themselves with difficulty against the hand that tries to seize them; that as soon as the sun goes down these animals seek their night shelter, the old adage, 'To go to bed with the hens,' meaning to go to bed early, evidently having its origin in this fact."[1]

Biological investigation appears to show, therefore, a co-existence of rods and visual purple with vision of the twilight type and of cones with optimal vision in daylight. Reasoning from analogy is, however, proverbially dangerous, and the importance of the facts described can easily be exaggerated. We have, and can have, no direct knowledge of the actual type of vision possessed by the animals mentioned; in some, notably the bat, it is a matter of doubt how far vision is the true directive sense under twilight conditions. The early roosting of diurnal birds may also be due to causes other than a state of night-blindness.

The whole case can be summed up in the following way:—

(1) There is a marked difference between central and peripheral vision in regard to the phenomenon of darkness adaptation, the former being little, if at all, affected in the process.

(2) These differences may be provisionally interpreted on the hypothesis that visual sensations are bound up with two distinct mechanisms: (*a*) That of the cones, with which

[1] *La Vision*, by H. Parinaud, Paris, 1898, p. 66.

chromatic responsiveness and colourless sensori-reactions in bright light are associated; (*b*) that of the rods, upon which depend achromatic reactions under conditions of darkness adaptation.

The objections to this view are neither few nor unimportant. It has not been proved that no central adaptation occurs. The equations (colour matches) of totally colour-blind persons and those of the normal "dark" eye agree well, but not completely.

The interpretation of the secondary image of recurrent vision is not complete.

The first of these objections, as well as the kindred one that a central scotoma does not exist in all cases of total-colour-blindness, may be parried by supposing that a trace of visual purple and a few scattered rods are present in the fovea. Recent measurements by Fritsch give an absolutely rod-free zone of only ·2 mm., corresponding to an angular distance of less than a degree. We must not attach much weight to failures in the demonstration of such small non-adaptable areas, even supposing that they are completely rod-free.

The difficulty regarding "total-colour-blindness" and normal "dark" equations is not formidable. Sufficient measurements have not been made to enable us to affirm that the differences are significant. The most serious difficulty as to the secondary image of recurrent vision has already been discussed; it may prove the crucial point of the theory.

If one adopts the above view of the rôle of the visual purple and rods as elements in the physiological processes of vision with low intensities of light, one is tempted to speculate as to the nature of their activity. We have, however, only negative evidence. We can say with some confidence that retinal fluorescence is not an important factor in the process; beyond this we cannot at present go.

In conclusion, the reader must clearly understand that the cones of the peripheral retinæ are not functionless, that peripheral vision in daylight is quite different from the type

studied in this chapter. The following table shows this very distinctly:—

Na line = 100.

Wave length . .	680	651	629	608	589	573	558	530	513
Peripheral value daylight . .	9·6	37·5	77·5	101	100	79·6	52·2	28·5	14·6
Peripheral value twilight . .	?	3·4	14·0	35·5	100	256	351	321	198

RECOMMENDED FOR FURTHER STUDY

The reader should consult the bibliography on pp. 376–7 of "Further Advances in Physiology." Of the papers mentioned, the most important are—

Die Helldunkeladaptation des Auges und die Funktion der Stäbchen und Zapfen, by *A. von Tschermak*, Ergebn. d. Physiol., 1st Jahrg. pt. h. pp. 695, etc.

J. von Kries, Die Gesichtsempfindungen, Nagel's Handb., vol. iii. pp. 109–282.

On Recurrent Vision, *Macdougall*, British Journ. of Psychol., i. 78; *v. Kries*, Z.P.P.S.O., xxix. 81; *Hess*, ibid., xxvii. 1.

CHAPTER XIV

TRICHROMATIC VISION

Up to the present we have considered visual sensations from the standpoint of pure comparison. Without analysing either the sensations themselves or their physical forerunners, we have been content to ascertain whether a physical agent of approximate constancy is or is not followed by the same phenomenon in consciousness irrespectively of the exact region stimulated or the general experimental conditions (light or dark adaptation). We have found that the end product does vary with the part of the retina examined and the latter's adaptive state. We now enter upon a wider and more difficult part of our inquiry, namely, a presentation and arrangement of the chief physiological facts of visual sensation. The difficulty of this task is apparent when one considers what is involved. We must attempt to describe the interplay of a complex of factors, physical, physiological, and psychological; some of these are fairly well understood, others hardly at all, so that we can frequently do little more than echo the words of a great master of the subject—"The confession of actual doubt is better than the delusion of dogmatic certainty."[1]

In the first place, are visual sensations *solely* dependent upon their physical forerunners? Under like physiological conditions and with equal physical stimuli are the responses identical? Reflection makes it clear that the answer is—no; what we term the colour of an object is not a simple percept, but a construct. The difficulty has been admirably put by Hering, whose remarks deserve close attention. He writes: "The layman is convinced that external objects possess definite colours, that snow is white, soot black, and gold yellow. He attributes to these colours an existence inde-

[1] Helmholtz, *Handb. d. Phys. Opt.*, p. 379.

pendent of the eye, and characterises them as the real (*wirkliche*) colours of the respective objects, distinguishing them from the accidental (*zufällige*) colours which the same objects exhibit under unusual circumstances, *e.g.* with insufficient illumination, or illumination differing very markedly from ordinary daylight. The red of the mountain peak in the Alpine glow; the corpse-like pallor of a face illuminated by the sodium flame; the bright spots on the floor of a room into which the sunlight streams through bright window-panes, are instances of such occasional colours which we attribute to a corresponding peculiarity of the illumination, and do not regard as characteristics of the objects in question. One who has learned that snow owes its whiteness and gold its yellowness to the particular rays of daylight reflected by each, easily forms the opinion that the "real" colour of external objects must be black, since he regards black, erroneously, as being due to a complete absence of light rays. Yet whenever he thinks of the snow, he always pictures it as white; and so do all of us, whether we have thought much or little about the nature of colours. Thus the mineralogist, to whom snow is a heaping together of little colourless transparent water crystals; the chemist, for whom these crystals are composed of countless atoms and molecules; the physicist, looking beyond atoms and molecules to forms of energy—all perforce associate with the conception of snow the white colour."[1]

It amounts to this then, the colour sensations usually experienced when we are stimulated by certain objects are supposed by us to be necessarily connected with these objects. "What the layman calls the real colour of an object is a colour of the object constantly present in his memory," and may be termed a "memory colour." The importance of such colours is obvious; they render it impossible for us to describe visual sensations completely in terms of any physical measurements, since the sensation value of a stimulus is not solely dependent on that stimulus considered by itself. Two stimuli of equal value—physically

[1] Hering, *Grundzüge der Lehre vom Lichtsinn*, Leipzig, 1905, p. 6.

speaking—will not necessarily elicit the same sensation even if compared under approximately the same physiological conditions. The different results which may follow the application of a constant stimulus are thought to be demonstrated by an experiment devised by Hering[1] (Fig. 14).

If the apparatus be arranged as indicated in the diagram, with a suitably chosen artificial light, both papers appear brown, the yellow working rays reflected from the blue paper overpowering the blue rays. If the window be now shut and, without altering the artificial light, the two pieces of paper be removed from the photometer and examined, it

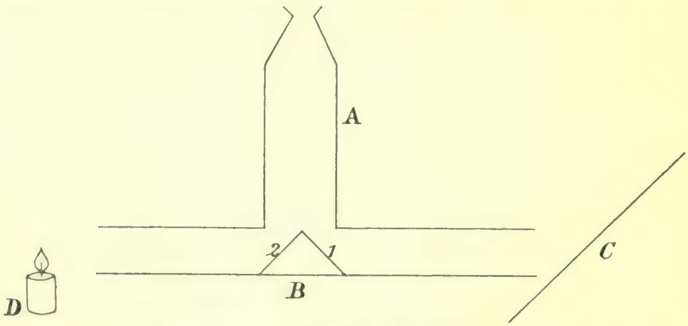


FIG. 14.—*A*. Wooden Photometer Tube. *B*. Cylinder with Wooden Prism having Blue and Brown (2 and 1) Papers on either side. *D*. Artificial Light. *C*. Mirror reflecting daylight.

will be seen that the "really blue" paper, although it is sending to the eye precisely the same mixture of rays as before, looks blue just as in daylight, only perhaps a little darker, while the brown paper still looks brown. In Hering's opinion, the constancy of colours in objects is one of the most striking phenomena in the field of visual sensations. Without it a piece of chalk on a dull day would have the same colour as a piece of coal on a sunny day, and, in the course of a single day, would pass through a remarkable series of gradations between white and black. The consequence would be that we should no more attribute whiteness to chalk or blackness to coal than hotness or coldness to iron.

Interesting as are these reflections, it is permissible to

[1] Hering, *op. cit.*, p. 15.

doubt whether the invocation of "memory colours" is necessary to account for the constancy of colour phenomena. It is equally reasonable to suppose that chalk never on the dullest day resembles coal, because relatively to coal it always reflects more white light. Hering's experiment appears to me to involve too many factors for us to regard it as demonstrating his theses. Even, however, if we accept Hering's view, it by no means follows that we ought to discard experimental methods founded upon physical measurements. In quite popular language, the position may be stated as follows: We look at two scraps of paper, and say that in one case we experience a sensation of blueness and in the other one of redness; we then find that vibrations of one type are predominately reflected by the one and of another type by the other object. Although we must *not* say that this difference in vibration period is the *only* cause of the sensational difference, it may be convenient to use it as some criterion. This experimental convenience is some justification for saying that colour tone depends on wave length, colour saturation on wave purity, and intensity on wave energy. I hope to show that, by adopting this convention, we can simplify our description of the facts without seriously prejudicing their theoretical interpretation. I shall therefore pursue the following order—the empirical methods and results of colour-mixing and the phenomena of after-images will be described; then the theoretical deductions which have been made from these results, together with experiments specially designed to test these deductions; and subsequently certain peculiar and special phenomena of colour vision will be considered.

The physical basis of this kind of work is to be found in the conception of a simple or homogeneous light, and dates from Newton's researches on prismatic analysis. By homogeneous light we are to understand ethereal vibrations, the wave lengths of which fall within certain narrow limits. Prisms and gratings enable us to filter such lights from a mixture, and to employ them for our experiments. A pure light is uniquely defined by its wave length, and any such light may possess any intensity. The physical unit of

intensity is not easily fixed, perhaps the best attempt being that of Krarup,[1] who has applied the energy measurements of Angström. In any spectrum the intensities of the individual lights depend on the source of illumination and the method of analysis, *i.e.* on the extent of surface over which light of a given wave length is spread. In an "interference" spectrum diffusion is uniform; in a prismatic spectrum, on the other hand, it increases from red to violet, so that the short-waved light is relatively less intense than the long-waved. Spectra obtained by the two methods are accordingly not directly comparable.

By colour or light mixing we understand an arrangement by which two or more homogeneous lights fall upon the same retinal area. That our experiments may be pure we

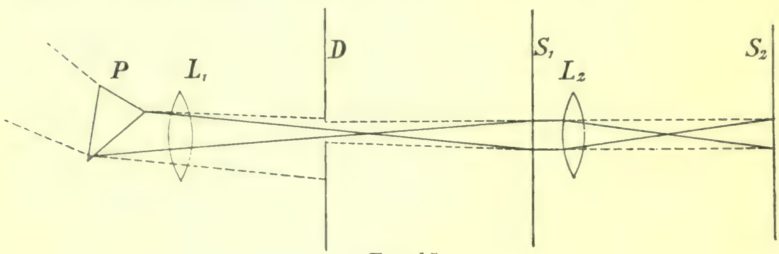


FIG. 15.

have to use pure light of constant intensity, which often necessitates the use of complex optical apparatus. Pigments cannot be used, because the light proceeding from a mixture of pigment is not equal to the sum of the lights emitted by the constituents, owing to selective absorption. A simple method, sufficient for many purposes, is the rotation of coloured sectors on a colour mixer such as is generally used for demonstrations. A more accurate method is that due to Helmholtz. Sunlight reflected from a heliostat enters a dark room by a slit, and then passes through a prism P (Fig. 15) and an achromatic lens L_1. The screen S_1 is placed in the focal plane of the eyepiece, and a spectrum projected upon its anterior surface. Between lens and screen a diaphragm D is inserted, and the screen is furnished with

[1] H. Krarup, *Physisch-opthalmologische Greuzprobleme*, Leipzig, 1906.

two vertical slits which allow definite portions of the spectrum to pass through. A second achromatic lens L_2, of somewhat shorter focal length, projects an image of the diaphragm upon a second screen S_2. The aperture of the diaphragm must be so small that each of the pure lights is distributed over the whole of it. Under these circumstances the field projected on the second screen is made up of a uniform mixture of the two colours; colour tone and intensity are varied by adjusting accurately the position and breadth of the slits.

Other more elaborate and exact methods can be used, but their description would be tedious. In most cases it is desirable to obtain a comparison as well as a mixed field, and this necessarily increases the difficulty of the arrangement.

Examination of a spectrum teaches us that, apart from extremes of intensity, change in wave length goes with change in chromatic quality or colour tone, provided the alteration in colour tone exceeds a lower limit. At the ends of the spectrum, however, increase in wave length above or diminution below a certain value is not accompanied by a corresponding sensation difference. The reason of this limitation is perhaps physiological, but its discussion must be omitted.[1]

Experiments carried out by one of the mixing processes just mentioned have enabled us to formulate certain general statements which were first clearly enunciated by Grassmann. These conclusions are as follows: If, in a mixture, one component be continuously varied, the appearance of the mixture will likewise vary (unequal lights mixed with equal lights produce unequal mixtures). If two lights look the same, then if each be mixed with a third light, the resultant mixtures will look equal. This can, of course, be generalised. A corollary is, that proportional increase of the intensity of each component in a mixture does not destroy a match.

Passing to the actual observations, we at once note that the effect of mixing spectral extremes is the production of

[1] See Krarup, *op. cit.*, pp. 15–19.

a colour—purple—not present in the spectrum at all. It thus follows that any graphical representation of our results must take the form of a closed curve, since passing from red to violet we can either travel over the range of spectral colours or by way of purple. If we mix lights not belonging to the extreme ends of the range, our results are quite different. The simplest cases are those of mixing colours of wave length not less than 540 $\mu\mu$. For instance, a red (670 $\mu\mu$) mixed with a yellow (580 $\mu\mu$) gives a pure colour of intermediate wave length. The greater the proportion of the long-waved component, the nearer will the position of the mixture approach the red end of the spectrum, and conversely. The mixing relations for this part of the spectrum are therefore quite straightforward; but the result obtained—*i.e.* that two simple lights when mixed give a simple light the wave length of which is intermediate between those of its components—is only valid for a small part of the spectral range. If we mix a blue-green (510 $\mu\mu$) with a blue (460 $\mu\mu$) the mixture, although resembling, perhaps closely, a pure intermediate—*e.g.* 490 $\mu\mu$—does not match it perfectly. The mixed colour is paler, or, as we say, "less saturated," than the spectral one. This is still more evident when we choose our colours in such a way that the wave length of one is greater and that of the other less than 517 $\mu\mu$. If one constituent is taken a little nearer the red than 560 $\mu\mu$, and the other diminished in each experiment, then, with suitable proportions, the mixtures pass from greenish-yellow—becoming paler and paler—until we reach a combination which corresponds to a sensation of whiteness. As we tend to assign a unique position to white in our sensation-scale, it is customary to complete the mixing laws by the following statement: Any light mixture whatever can be matched by a mixture of a definite homogeneous light (or a definite purple) and white light. That our results may be as general as possible, it is well to note that there is no necessity for according a special place to white.

"If we regard any homogeneous or compound light whatever as fixed, and then mix it with the whole series of pure lights completed by purple, at the same time varying the

proportions in the mixture from the zero of the one to that of the other, we obtain all possible varieties of stimuli; that is, any possible combination is matched by some member of the series." [1]

It is, however, convenient in practice to separate white, and I shall continue to follow the usual classification.

We have seen that our mixing experiments give us variations in colour tone and variations in whiteness—that is, two variables—so that our results should be expressible graphically by some plane figure. We have also noticed that we can pass from red to violet, and then from violet again to red, without passing through the spectral range more than once, so that our graph should be a closed figure; finally, in virtue of the fact that the position of any mixed colour depends directly upon the relative proportions of its components, we infer that the method of obtaining the position of the centre of inertia of masses is applicable. If three colours, A, B, C, none of which can be mixed from the other two, be represented by three points in a plane, then, on assigning to them values in terms of any unit, the situations and quantitative values of their mixtures can be ascertained. Thus a colour mixed from a parts of A and b parts of B will lie on the line A B at the point at which the centre of inertia of the two masses a and b (representing the proportions of the two colours in the mixture) would be situated. In order to establish the correctness of this method it is necessary to prove that, given the experimental laws of colour-mixing, this construction is valid in all possible cases, *i.e.* that the situation of the mixed colour coincides with that of the mass centre of two equivalent masses (1) when the two constituents can be mixed from the three chosen colours, (2) when one can and the other cannot so be mixed, (3) when neither can so be mixed. The proof is too long for insertion in a book of this size, but it requires only an elementary knowledge of mathematics for its comprehension.[2] We can show that the co-ordinates of the point at which the mixture must be situated according to the mixing laws are the co-ordinates of the

[1] J. v. Kries, Nagel's *Handb.*, vol. iii. p. 116.

[2] See Helmholtz, *Phys. Optik.*, second edition, pp. 328–330.

mass centre of weights situated at the points where the components lie.

It is clear that a diagram constructed on these principles will vary in its actual form in accordance with our choice of units and fixed points. Thus Newton chose white as a fixed point, and arranged the simple lights at equal distances from it, so that the diagram was a circle; we should obtain this result, except that the part of the curve passing from violet to red must be a straight line, since purple can only be mixed from violet and red, and its representation must be on the chord joining their representative points. If we recur to our experimental results, however, we shall see that the best diagram to adopt is that figured 16. From red to

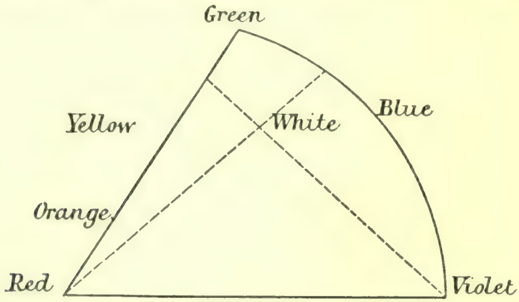


FIG. 16.—Colour Table.

yellow the curve is a straight line, since we found that mixtures of colours between those limits matched pure spectral lights. We then get a sharp flexure in the part of the diagram beyond green, representing the low saturation of mixtures from this region, and finally we have the straight line through purple.

Suppose now we select three colours in the spectral series, *e.g.* red, green, and blue, then in accordance with our previous deductions all mixtures of these are represented in the triangle R, G, B (Fig. 17); this includes a good deal of our complete diagram, but not all of it. If we choose red, green, and violet, the triangle R, C, V includes nearly the whole spectral diagram; in other words, nearly all spectral colours can be matched by mixing three chosen lights in suitable proportions.

There is not indeed a complete coincidence, because of the bend in the spectral figure between green and blue, which means that mixtures of green and violet are less saturated than spectral cyan blue ; we can, however, generalise a little. If spectral greenish-blue be mixed with red in certain proportions, it matches a mixture of green and violet, or

$$a\mathrm{GBl} + \beta\mathrm{R} = \gamma\mathrm{Gr} + \epsilon\mathrm{V}.$$

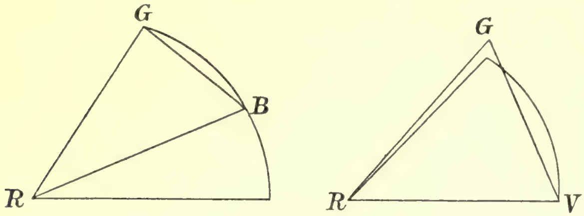


FIG. 17.

Hence $a\mathrm{GBl} = \gamma\mathrm{Gr} + \epsilon\mathrm{V} - \beta\mathrm{R}$, or we have the unmixable colour in terms of our three chosen colours. I do not, however, think this mode of expression desirable, since it is hardly capable of objective interpretation. It is to be remarked that colour equations, as they are termed, of the form $\mathrm{R} + \mathrm{Gr} + \mathrm{V} = \mathrm{R}$, seem to be justifiable ways of expressing experimental facts. Addition is uniform, the same result being always obtained when the same quantities are summed ; it is commutative, the order of operations does not affect the result ; it is associative and homogeneous. These characters are found in our mixing process. Green + (mixed with) red + (mixed with) violet = (match) red + green + violet = (red + violet) + green. If we define subtraction, *in terms of arithmetical quantity*, as uniform, non-commutative, and non-associative, similar analogies can be observed ; but this is of little importance, since a justification of the use of the symbol of addition will suffice for our purposes.

We can now consider some experimental points. Since, practically, all chromatic stimuli may be expressed in terms of three, researches are conducted in the following way: A definite spectrum—*e.g.* the prismatic spectrum of an Auer gas lamp and three lights—*e.g.* a red, a green, and a blue of arbitrary but constant intensity are selected. Each part of the

spectrum is then matched by mixing the three together until the mixed colour looks exactly like the homogeneous one. This process of spectral gauging has been applied by Koenig and Dieterici[1] to the investigation of normal colour vision, and their results are generally regarded as correct. Experiments involving the manipulation and mixture of three pure lights are beset with technical difficulties, and the results are not entirely free from objection, so that I do not propose to give details, especially in view of the fact that we can, for many purposes, obtain almost as much information by another method. All I desire to emphasise is the general conclusion that the experimental facts of colour vision can be graphically represented by a plane figure, and the possible forms of stimuli reduced to terms of three independent variables—that is to say, normal colour vision is trichromatic.

It is important to notice that a choice of variables is, from the theoretical standpoint, arbitrary; indeed, if a table be constructed in terms of three primaries, A, B, C, a second can be deduced in terms of another three, A′, B′, C′, because in view of what has gone before, it is plain that we can always define A′ by an equation of the form $A' = aA + bC + cC$, and similarly for the other variables, the process merely involving a change of co-ordinate axes. Clearly, if we choose our primaries so near together that we cannot experimentally reproduce all the spectral stimulus values, our table will involve negative directions, but this is of no theoretical importance.

Although, as I have said, it is not necessary to give full details as to spectral gauging, I may note the results obtained with complementaries. The usual definition of complementary colours—*i.e.* two lights which, when mixed together, give a colourless mixture—is ambiguous, depending on whether we define white subjectively or by reference to a mixture of known physical composition. Experimentally, the results obtained with and without a comparison field of known composition, *i.e.* by the second or the first method, do not differ widely. The table contains the values ascertained by Helmholtz (without a comparison), and those of

[1] *Z.P.P.S.O.*, iv. 292.

Complementary Colours for Two Observers.

Observer, v. Kries.		Observer, v. Frey.		Helmholtz.	
Long-waved Light.	Short-waved Light.	Long-waved Light.	Short-waved Light.	Long-waved Light.	Short-waved Light.
μμ	μμ	μμ	μμ	μμ	μμ
656·2	492·4	656·2	485·2	656·2	492·1
626	492·2	626	484·6	607·7	489·7
612·3	489·6	612·3	483·6	585·3	485·4
599·5	487·8	599·5	481·8	573·7	482·1
587·6	484·7	587·6	478·9	567·1	464·5
579·7	478·7	586·7	478·7	564·4	461·8
577·6	473·9	577·7	473·9	563·5	From 433 downwards
575·5	469·3	572·8	469·3		
572·9	464·8	570·7	464·8		
571·1	460·4	569·0	460·4		
571·0	452·9	568·1	452·1		
570·4	440·4	566·3	440·4		
570·1	429·5	566·4	429·5		

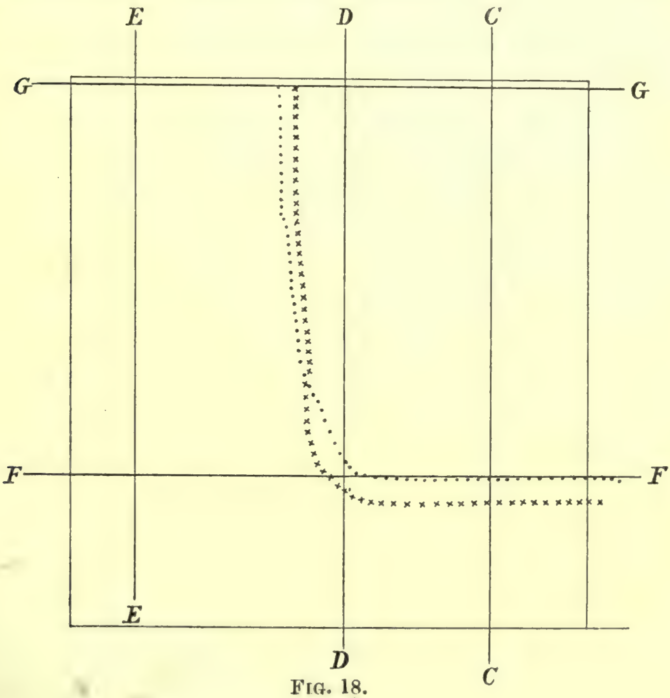


Fig. 18.

v. Frey and v. Kries (with a comparison). The diagram is constructed from the second series. It will be seen that, at the red end, as the wave length changes, that of its complementary changes at first very slowly, then faster, until finally very great changes in wave length are associated with relatively little alterations in colour tone, while at the middle of the range the converse statement is true.

It will have been noticed in the diagram that the two observers do not agree exactly in their values, and some of these personal variations are of interest. The best-known illustration is afforded by the individual differences found in matching a homogeneous yellow by a mixture of red and green; a good match for one eye is too green for another, too red for a third. Maxwell, who first noticed this, suggested that the differences depend upon unequal quantities of yellow pigment in the macula, since yellow pigment absorbs very little long-waved light, only becoming markedly active for the yellow-green region of the spectrum, its powers diminishing again towards the violet. The correctness of this suggestion has been rendered highly probable by the researches of Hering, Sachs, v. Frey, and v. Kries. It has been shown that (1) the variations are consistent with the hypothesis that the eye contains an absorbing pigment; (2) the macular pigment behaves as a yellow pigment from this point of view (Sachs); (3) the amount of macular pigment is variable; (4) finally, a red-green mixture which matches a homogeneous yellow on direct fixation appears too green when examined paracentrally, and the central equation $R + BlG = V$ appears distinctly bluish-green in indirect vision. These differences are therefore of a physical order, and need not detain us.

There are, however, in addition some cases which cannot be brought under the last category. Lord Rayleigh discovered that when testing the equation Homogeneous Yellow = Red + Green, certain persons required more red and others more green than the majority. These results have been confirmed by Donders, Hering, v. Kries, Koenig, and Dieterici, the type requiring an excess of green being the more frequent. These forms of trichromatic vision have been termed by v. Kries the anomalous greens and the

anomalous reds, and it is certain the peculiarities do not depend simply on physical differences. If the changes were due to differences in pigmentation, then, in matching a red-green mixed with homogeneous lights from 670 $\mu\mu$ to 570 $\mu\mu$, these subjects would require throughout the same proportional increase in the green component of the mixture, which is not the case. Similar typical differences are observed in peripheral matches. These results prove that distinct variations in trichromatic vision exist which are irrespective of differences in macular pigmentation, but perhaps no advantage is obtained by assigning them to separate classes. Hering in examining the colour sense of a series of persons found they could be divided roughly into two groups, one set making the brightness match, Spectral red (660 $\mu\mu$): Spectral blue (447 $\mu\mu$) : : 1.15 : 1; the other for the same match requiring the discs in the ratio of 7 to 1. The spectral light judged to be pure green was not the same in the two classes, but nearer the red end in the first group. There were also typical differences in the composition of colourless red and bluish-green or greenish-yellow and violet mixtures; in each case the first group required relatively large quantities of the short-waved component. The first group were said to be relatively yellow sighted, the second relatively blue sighted, in allusion to their special responsiveness to these colours; v. Kries' red anomaly would be an extreme case of yellow sightedness, his green anomaly a marked example of blue sightedness. It is therefore not improbable that these abnormal trichromatics are extreme variants of a frequency system representing the whole range of visual types. The matter can only be settled when the quantitative mixing ratios for a definite match have been determined on a large number of persons taken at random; we may then find that the results are in accordance with some well-known frequency distribution, the normal equation representing a modal value. At present, the theoretical interpretation of these cases is extremely difficult. Summing up the results obtained in this chapter, we see :—

(1) A complete sensational analysis of vision cannot be effected in terms of stimuli.

(2) Fixing our attention on stimuli only, mixing results are functions of two variables, and graphically expressible by means of a plane figure.

(3) Colour differences can be expressed in terms of three chosen stimuli, the choice being theoretically restricted, but in practice certain definite stimuli are conveniently chosen.

(4) Of the discrepancies observed between the matches of certain individuals, some depend on peculiarities of physical structure; others are to be provisionally regarded as extreme variants from a modal type of vision.

I hope to have made it clear that these statements are essentially descriptive, designed to resume experimental facts as simply as possible. Colour diagrams and the assertion that normal colour vision is (roughly) trichromatic are short ways of expressing experimental results, and contain no hidden theoretical meaning; their truth, or falsehood, is a matter of observation. As we shall see later, the results have been the starting point of various hypotheses regarding the nature of visual processes, but the success, or failure, of these attempts is quite another story.

In the next chapter we shall treat in the same objective fashion of those examples of partial colour-blindness which are physiologically interesting, and shall find that, just as normal vision may be called trichromatic, these types are dichromatic.

RECOMMENDED FOR FURTHER STUDY

Hermann v. Helmholtz, Handbuch der Physiologischen Optik., second edition, 1896, pp. 311–341. (The classical work, one of the greatest books of any age, contains full bibliography up to 1895.)

Ewald Hering, op. cit. (Most suggestive and readable.)

J. v. Kries, Nagel's Handb., vol. iii. 109–127.

Sachs On Macular Pigment, Pflüg. Arch., vol. l. p. 574.

J. v. Kries, Beitr. z. Phys. d. Gesichtempf., Du Bois R. Arch. f. Phys., 1878, p. 503.

Lord Rayleigh, Experiments on Colour, Nature, 1881, p. 264.

Donders, Du Bois R. Arch. f. Phys., 1884, p. 518.

J. v. Kries, Z.P.P.S.O., vol. xiii. p. 241, and vol. xix. p. 63.

W. Nagel, Arch. f. Augenheilkunde, vol. xxxviii. p. 31.

CHAPTER XV

DICHROMATIC VISION

WE have seen that, from the purely experimental point of view, the characteristics of normal colour vision admit of relatively simple arrangement, that, in fact, all the results of stimulation can be expressed in terms of three different stimuli; we must next consider some types of vision which, if themselves abnormal, throw light on the normal mechanism.

The existence of abnormal visual systems is known to have been recognised for more than two centuries,[1] but John Dalton, the great chemist, was the first to attract much attention to the subject.[2] Goethe in his *Farbenlehre*, which appeared in 1812, gave the following description :—

"We will here first advert to a very remarkable state in which the vision of many persons is found to be. As it presents a deviation from the ordinary mode of seeing colours, it may fairly be classed under morbid impressions; but as it is consistent with itself, as it often occurs, may extend to several members of a family, and probably does not admit of cure, we may consider it as bordering only on the nosological cases, and therefore place it first. I was acquainted with two individuals not more than twenty years of age who were thus affected. . . . They agreed with the rest of the world in denominating white, black, and grey in the usual manner. . . . They appeared to see yellow, red-yellow, and yellow-red like others. . . . But now a striking difference presented itself. If the carmine was pressed thinly over the white saucer, they would compare the light colour

[1] Turberville, *Phil. Trans.*, 1684; Huddart, *Phil. Trans.*, 1777; Whison, *Phil. Trans.*, 1778.

[2] J. Dalton, *Literary and Philosophical Society of Manchester*, 1794. (Cited in Koenig's bibliography.)

thus produced to the colour of the sky, and call it blue. If a rose were shown them beside it, they would in like manner call it blue; and in all the trials that were made, it appeared that they could not distinguish light blue from rose colour. They confounded rose colour, blue, and violet on all occasions: these colours only appeared to them to be distinguished from each other by delicate shades of lighter, darker, intenser, or fainter appearance. Again, they could not distinguish green from dark orange, nor, more especially, from a red brown.

"If any one, accidentally conversing with these individuals, happened to question them about surrounding objects, their answers occasioned the greatest perplexity, and the interrogator began to fancy his own wits were out of order. With some method we may, however, approach to a nearer knowledge of the law of this deviation from the general law.

"These persons, as may be gathered from what has been stated, saw fewer colours than other people; hence arose the confusion of different colours. . . ."[1]

Since the time of Goethe a great deal of attention has been devoted to the subject, and its literature has attained formidable proportions.

The most obvious distinction between the vision of the partially colour-blind and our own is an inability to perceive differences which are plain to us. As Goethe says, such persons see fewer colours than we do. This difficulty is of special interest, because it is something definite; it is comparatively easy to find out whether a person can distinguish between the effects produced on him by two stimuli which certainly affect us differently, while the actual physiological or psychological nature of the effect may remain obscure. How a certain green light affects a colour-blind eye, by what sensation it is followed, we can only guess, but we know that the effect is indistinguishable from that produced by a certain intensity of red light. We have, then, to deal with a condition in which the conscious responses

[1] Goethe's *Theory of Colours*, translated by Eastlake, pp. 45–7. London, 1840 (Murray).

to varied physical stimuli are fewer than in normal persons. The question is, whether the experimental results can be summed up in the simple manner that was possible in the case of normal vision. It will be found that, with certain limitations, the results can be so described.

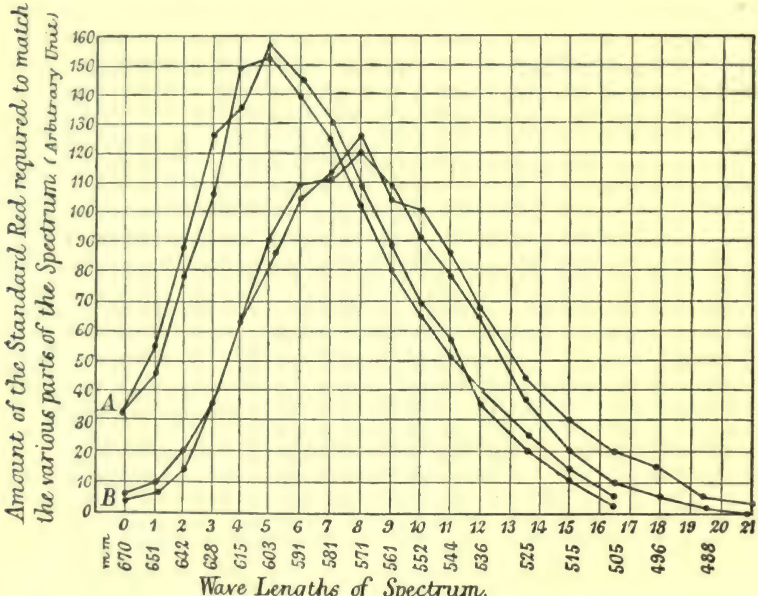
We learned that for most experimental purposes normal colour is expressible in terms of three colours. The vision

Proportions of Standard Red and Blue in a Mixture of apparently the same Tint as various Spectral Colours in four cases of Partial Colour-Blindness (v. Kries).

Spectral Wave Lengths in millionths of a millimetre.	Deuteranope (1).		Deuteranope (2).		Protanope (1).		Protanope (2).	
	Red.	Blue.	Red.	Blue.	Red.	Blue.	Red.	Blue.
670·8	33·0	...	34·4	...	5·3	...	4·9	...
656·0	48·0	...	56·4	...	9·1	...	8·4	...
642·0	79·0	...	95·0	...	19·0	...	18·0	...
628·0	107·0	...	126·0	...	38·0	...	38·5	...
615·0	147·0	...	138·0	...	63·0	...	63·0	...
603·0	151·0	...	155·0	...	90·0	...	84·0	...
591·0	137·0	...	144·0	...	109·0	...	105·0	...
581·0	124·0	...	129·0	...	111·0	...	113·0	...
571·0	103·0	...	108·0	...	120·0	...	126·0	...
561·0	82·0	...	89·0	...	108·0	...	106·0	...
552·0	64·0	...	65·0	...	2·0	...	101·0	...
544·0	52·0	...	56·0	...	78·0	...	85·0	...
536·0	41·0	6·3	37·4	6·0	65·0	...	67·5	...
525·0	26·0	12·0	21·0	10·3	38·3	11·0	46·8	...
515·0	15·0	28·0	13·7	21·6	20·6	34·0	32·8	13·0
505·0	7·7	36·0	7·5	32·2	9·8	35·0	17·2	29·0
496·0	3·7	48·0	4·1	46·3	4·8	47·0	8·4	33·0
488·0	1·6	62·0	1·9	58·0	2·2	57·0	5·3	49·0
480·0	0·9	64·0	0·9	67·0	0·9	66·0	2·9	71·0
469·0	0·3	70·0	0·3	65·6	0·3	67·0	1·0	69·0
460·8	...	67·0	...	68·6	...	54·0	...	66·0

of partial colour-blinds is expressible in terms of two. If we choose as our fixed lights a red and a blue, these, mixed in certain proportions, will match every part of the spectrum as it appears to the partially colour-blind, and also unanalysed daylight. Normal colour vision is trichromatic, this is dichromatic. But, just as the required proportions in the mixture differed in various types of trichromatic vision, we also find two types of dichromatics, distinguished by their

respective mixing ratios. The two classes are known by various names, of which I shall employ Protanope and Deuteranope as being quite non-committal from the theoretical standpoint. Experimentally one proceeds just as in the examination of normal colour vision. A certain red and a certain blue are chosen, and the whole spectrum systemati-



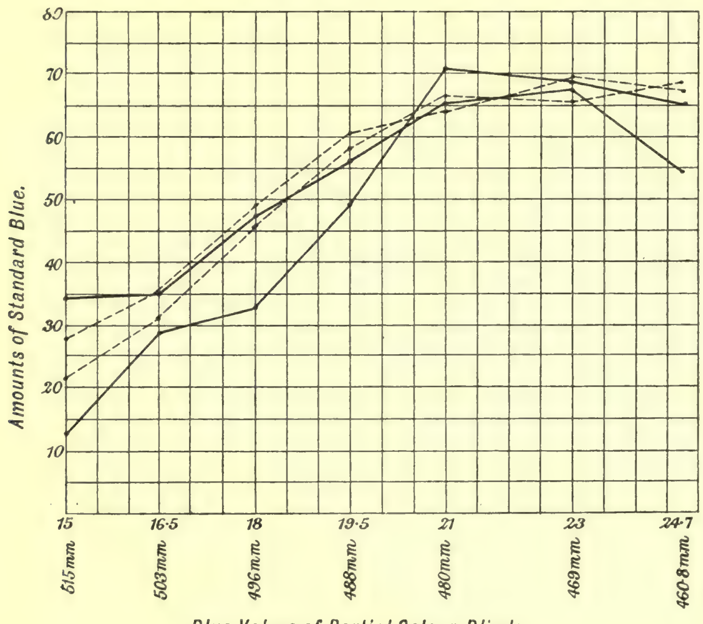
Red Values for Partial Colour Blinds (v Kries).
The two curves A are Denteranopes, the two B Protanopes.

cally matched against various mixtures of the chosen standard lights. The tables and diagrams embody the results of J. v. Kries.[1]

An examination of the curves shows that the cases fall into two groups in respect of red values. The four blue value curves, on the other hand, are not very dissimilar; in fact, remembering that the physical differences of macular

[1] "Ueber Farbensysteme," *Z.P.P.S.O.*, vol. xiii. pp. 241–324. An abbreviated account, with the diagrams, by the same author in Nagel's *Handbuch d. Physiol. d. Menschen*, Braunschweig, 1905, vol. iii. pp. 153–55. Some account of the experimental technic will be found in *Z.P.P.S.O.*, vol. xii. pp. 4, etc.

absorption would be most influential in the part of the spectrum where the blue curves agree worst, we may regard the similarity as fairly close. Referring to the tables, we see that for matching spectral colours of wave length greater than 530 $\mu\mu$ no blue at all is required, so that the forms of the red value curves beyond this point are especially instructive. In one group the curve rises fairly sharply to a maximum about 571 $\mu\mu$ and then falls steeply, suggesting



Blue Values of Partial Colour-Blinds.

a relatively low stimulus value for the long-waved light; in the other group the rise is more gradual, attaining a maximum at 603 $\mu\mu$, while the curve does not fall to so low a point at the red end. Hence, within the region under examination, we may say, with fair accuracy, that the four subjects are grouped into one pair relatively more sensitive to short-waved light and one pair relatively more sensitive to long-waved light. To the former group we apply the name Protanopes, to the latter that of Deuteranopes. But, it may be objected, we have only examined four cases. It

is necessary to see whether the results attained are confirmed when experiments are carried out on a larger scale. If the conclusions just stated be valid, in matching yellow some partial colour-blinds (protanopes) will require enormously more red than others (deuteranopes). This is a test which can be quickly applied, while the above examination is too elaborate to be often repeated. V. Kries tested twenty cases, using red (lithium line) and a fixed yellow (sodium line). The results are contained in the table below, and it will be seen that one set (protanopes) required on the average five times as much red as the other group (deuteranopes) to match

Protanopes.	Deuteranopes.
214·0	36·5 [1]
213·0	36·3 [1]
211·0	36·3 [1]
205·0	36·5 [1]
196·0	38·4
198·0	37·3
210·0	37·0
200·0	37·0
210·0	37·8
203·0	37·0
225·0	36·9
...	38·0

the standard yellow. There is, accordingly, some evidence that the classification is a definite one.

The relative insensitiveness to long-waved light explains the observation that in protanopes, who correspond to the class (badly) named red blinds, the red end of the spectrum appears shortened, although the shortening is of very little importance from our point of view. It is to be remarked that within each class slight individual variations are found. In the two protanopic cases, from 552 $\mu\mu$ onwards to violet, one subject constantly demanded more red in his mixture than the other.

An interpretation is easy: in the observer requiring less red, the homogeneous light was probably weakened by macular absorption, since the diminution in red values agrees

[1] One subject.

with the known increments of absorption as we pass towards the violet. This difference is of some importance in connection with an interesting peculiarity of dichromatic vision. Since daylight can be matched, for the dichromatic eye, by a mixture of red-blue, and since all spectral colours can be matched by mixing the same two standards in varying proportions, we should expect some spectral colour to match, more or less closely, unanalysed daylight, and to appear to the dichromatic the same as what we call white or grey. Such a point of the spectrum is called "the neutral point." As for protanopes, the stimulus value of the light falls off rapidly towards the red; their "neutral point" should be nearer the violet than that of the deuteranopes; this is, in fact, generally the case, but if there is a good deal of pigment in the macula lutea, the mixed light undergoes selective absorption, and the homogeneous match is nearer the red end of the spectrum. Owing to this fact, the typical difference in the situation of the neutral point may not be found at all. The table on p. 146 gives results obtained on a deuteranope with a moderately pigmented macula, on a protanope with much and a protanope with little pigment in the macula region. Evidently simple determination of the neutral point would not enable us to distinguish the two forms.

A study of the neutral point, however, immediately brings to our notice that characteristic which has attracted the attention of practical men. Spectral light between 490–500 $\mu\mu$ induces normally the sensation of green; for the dichromatic it has the same effect as unanalysed daylight or a particular mixture of red and blue. But this mixture contains much red and little blue, so that a normal person asked to name the simple colour which it most resembled would say red. In other words, both the dichromatic classes confuse red and green. Even here we observe a class difference. In matching a given bluish-green the protanope, being relatively insensitive to long waves, requires much red in his blue-red mixture; the deuteranope takes about the same amount of blue, but much less red. Accordingly, a protanope confuses a light bluish-red (physically speaking) with a green that appears to us much darker, *e.g.* a scarlet with an olive-

green; a deuteranope matches a much bluer-red with green, which we should take to be about equally bright. Although both groups confuse certain reds with certain greens, "the red that appears equal to a given green differs markedly both in colour tone and intensity in protanopes and deuteranopes" (v. Kries). The fact that both forms of common colour-blindness are associated with a confusion of red and green is of great practical importance, since these colours are universally employed for signalling in connection with railways and ships. In most countries persons desirous of acting as engine-drivers or navigating officers are submitted to examination with a view to the detection of colour-blindness.

Neutral Points (v. Kries)

Mixed Light Used.	Wave Length (in $\mu\mu$) of the homogeneous Match.		
	Deuteranope.	1st Protanope.	2nd Protanope.
Magnesium oxide in daylight	499	498	490
Mirrored cloud weakened by ground glass	499	497	489
Do. do. weakened by smoked glass	495	494	486

While it is not the function of a theoretical writer to discuss at length a matter of this kind, a few remarks on the utilitarian aspect of the matter are not, perhaps, out of place. A test which can be easily applied, and is consequently dear to the mind of lay officials, is that associated with the name of Holmgren. The subject is given a large number of skeins of wool, and is told to separate out the reds and greens. This test is, in my opinion, altogether inefficient. Under the conditions of the test, the marked differences in luminosity of the wools often enables persons who suffer from typical colour-blindness to sort out the skeins correctly, especially if they have previously practised the experiment. Such

persons, however, would be highly dangerous navigators or engine-drivers, because at times when the differentiation of a red from a green light is vital, *e.g.* in a slight haze or in snowy weather, such adventitious aids as differences of intensity, apart from colour tone, will be absent. Edridge Green, to whom we owe many important observations on these points, has perfected a lantern test which is in every way superior to that of Holmgren, and nobody who takes on himself the responsibility of testing colour vision for administrative purposes can safely rely on the other and less efficient method. For further details, special works must be consulted.

Returning to the physiological characters of the two common types of colour vision, we have to consider what relations their visual systems bear to that of normal persons. The mere fact that the systems are dichromatic tells us comparatively little; we should indeed conclude that sensations of colour are less numerous for dichromatics than for us, but they might be quite different. What we seek is a relation between stimuli. As early as 1837 Seebeck expressed the opinion that two lights or mixtures of lights which appeared equal to the normal eye never appear unequal to colour-blind eyes, that equations valid for the normal eye are always valid for the colour-blind eye. If this be true, it is important, because in that event a dichromatic lacks something the normal person has, but possesses nothing the normal man has not got; in other words, dichromatism is an error of defect.

Experimental evidence, particularly that furnished by v. Kries, *on the whole* bears out Seebeck's view. In the first place, mixtures of red (670·8 $\mu\mu$) and yellowish-green (550 $\mu\mu$) which match a homogeneous yellow when the proportions are chosen to give a good match for a normal eye, give also equality for either a deuteranopic or protanopic subject. Similarly, any match which is found to be valid for both types is described as a good match by a normal person. "One employs the frequently cited equations between a homogeneous yellow and a mixture of red and yellowish-green (670·8 $\mu\mu$ and 550 $\mu\mu$). As all lights in this region are of

equal stimulus value for the colour-blind whatever the ratio of red to yellowish-green, one can always give the homogeneous yellow such an intensity that the match is good either for a protanope or a deuteranope, but in general the matches of the one are not valid for the other. As we should expect, a strongly red mixture is for the protanope equivalent to a yellow of relatively feeble intensity: a deuteranope finds in a match arranged by the protanope the mixture too bright and the pure yellow too dark. The relation is reversed for strongly green mixtures. With extraordinary accuracy, however, we find that for the ratio of red to yellowish-green that has for the trichromatic an equal colour tone with the homogeneous yellow, both groups agree; trichromatic equations are valid for both protanopes and deuteranopes. Conversely, if we try to find an equation valid for both groups, we arrive precisely at the one valid for a normal person."[1]

Still stronger evidence is afforded by the following considerations:—v. Kries prepared a table giving the mixing ratios for a normal person, matching spectral colours between 670·5 and 550 $\mu\mu$. The following are his results:—

Spectral Region.	Proportions of Standard Colours.	
Wave Length.	670·8 $\mu\mu$.	552 $\mu\mu$.
670·8	88·5	...
628·0	251·0	10
615·0	276·0	27
603·0	270·0	49
591·0	202·0	67
581·0	123·0	76
571·0	73·0	91
561·0	21·0	80
552·0	...	71

He also found that a certain deuteranope required 33 units of the standard red to match the spectral 670·8, and 64 units of the standard 552 to match the spectral 552 $\mu\mu$.

If deuteranopic vision is a reduction form of the normal

[1] V. Kries, Nagel's *Handb.*, iii. 160.

system, it should be possible from these data to calculate the stimulus values of intervening lights. Take as an illustration 591 $\mu\mu$, which is matched by 202 units of 670·8 $\mu\mu$ plus 67 units of 552 $\mu\mu$. We first change from the arbitrary intensity units of the normal subject by dividing by 88·5 and 71 respectively, and then express in the intensity scale of the deuteranope by multiplying by 33 and 64 respectively. The stimulus value should therefore be

$$\frac{202}{88\cdot5} \times 33 + \frac{67}{71} \times 64 = 135 \text{ (approx.) units.}$$

This, then, is the stimulus value of 591 $\mu\mu$ expressed in the intensity values of 670·8 $\mu\mu$ and 552 $\mu\mu$ for the given spectrum, on the hypothesis that a match good for a trichromatic eye is valid for a dichromatic; the observed value was 137. In this way the following table was obtained, and the agreement is very good:—

Stimulus Values for Deuteranope and Protanope.

Wave Length.	Deuteranope.		Protanope.	
	Calculated.	Observed.	Calculated.	Observed.
670	33	33	4·9	4·9
628	106	107	28·8	38·5
615	126	145	54·2	63·0
603	145	151	86·0	84·0
591	135	137	108·0	105·0
581	114	124	117·0	113·0
571	110	103	137·0	126·0
561	76	82	111·0	106·0
552	64	64	101·0	101·0

A further, but less satisfactory, verification is afforded by the construction of a normal colour table from observations made upon dichromatics. Bearing in mind the principles upon which the normal colour "triangle" depends, it is clear that in applying the method to dichromatic systems all those colours which appear alike to the colour-blind eye must lie on a straight line, since the line joining two points in the colour "triangle" contains all points corresponding to

colours which can be mixed from the colours represented by the first pair. It is also clear that the mixtures of confusion colours with any other colours lies on a series of straight lines. Hence it can be shown[1] that (1) all such lines meet in a point or are parallel, (2) the point of intersection corresponds to a colour which has no stimulus value for the colour-blind eye. This point is usually termed the "Fehlpunkt" of the system.[1]

Bearing these preliminaries in mind, the method of constructing a colour "triangle" for normal vision from dichromatic observations is simple.

Let ABC be an equilateral triangle, then it is *assumed* that the protanopic red value, the deuteranopic red value, and the common blue value are independent one of another, and their representative points are the apices of the triangle. The positions of the various lights are then determined in the following manner: Take, for instance, 603 $\mu\mu$. The protanopic red value is 90, the deuteranopic red value 155, the blue value 0. Divide AB in C′ so that AC′ : C′B = 90 : 155.

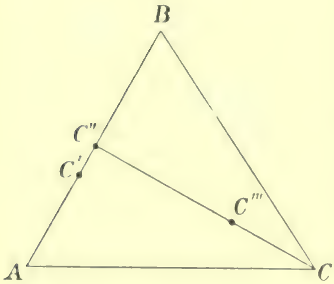


FIG. 19.

C′ marks the situation of 603 $\mu\mu$ in our "triangle." Take again 505 $\mu\mu$. The protanopic red value is 7·5, the deuteranopic red value 9·8, the blue value $\frac{32{\cdot}5 + 35}{2} = 33{\cdot}75$. Divide AB in C″ so that AC″ : C″B = 7·5 : 9·8. Join C″C; divide C″C in C‴ so that C″C‴ : CC‴ = 33·75 : 9·8 + 7·5. The diagram above shows a colour "triangle" constructed in this way by v. Kries. The only modifications are that (1) the unit for blue values has been increased fivefold, *i.e.* the tabled values (p. 149) have been divided by five for convenience of reproduction; (2) "the very small W (red) values for lights of wave lengths less than 505 $\mu\mu$ are not sufficiently exact to permit of the evaluation of the ratio

[1] See proof at the end of the chapter.

(protanopic red value : deuteranopic red value) with certainty. On this account, that part of the boundary line extending from blue to green would be correspondingly irregular, whereas observations on normal sighted persons show that it must present a steady curvature, mixtures of the two lights appearing a little less saturated than the spectral lights. I have for this reason drawn the boundary line with a constant curvature, so that the ratio gradually passes from that corresponding to lights between 515 $\mu\mu$ and 525 $\mu\mu$ to that observed for lights from 469 $\mu\mu$ to 480 $\mu\mu$. These two values are indicated in the drawing by the dotted lines from C; accordingly a curve drawn in exact correspondence with the observations would run irregularly between these lines. It should also be remarked that a construction of

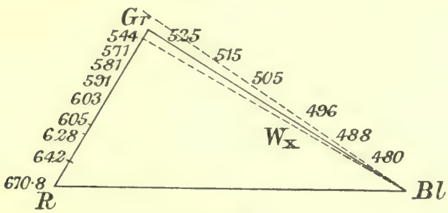


FIG. 20.

this sort is not entirely free from objection, as it combines the results of several observers with undoubtedly different amounts of macular pigmentation."[1]

That the process is not so satisfactory as the one already considered will be readily admitted. But we notice again that the deduced "triangle" agrees very fairly with that given in the chapter on trichromatic systems, so that it affords some confirmation of the surmise that dichromatic systems are in reality reduction forms of the trichromatic type.

The reader is specially cautioned that the conclusions hinted at in the last few pages are not to be pushed too far; for reasons, some of which will be considered in the chapters on theories, all the prominent workers of to-day recog-

[1] V. Kries, Nagel's *Handb.*, iii. 162.

nise that partial colour-blindness cannot be completely or adequately described in terms of a hypothesis postulating so simple a relation as that just suggested between normal and abnormal kinds of vision. The experimental results are, however, by no means without interest, and I have for that reason devoted some space to the matter. Summing up the rather difficult topics dealt with in this chapter, we may say that—

(1) The two common forms of partial colour-blindness are distinguishable one from another by varying responsiveness to long-waved and medium-waved lights. Protanopes are relatively insensitive to long waves, deuteranopes to short waves.

(2) Each is an example of dichromatic vision, using that term in a strictly experimental sense.

(3) Each is, very approximately, a reduction form of normal trichromatic vision.

The forms of partial colour-blindness just described are of everyday occurrence, and their recognition of obvious practical importance; another type, less common, and therefore less completely studied, is that known as Blue or Yellow-Blue Blindness. This condition, unlike the last, is not always congenital, and frequently one-sided. Definite pathological changes in the retina have also been observed in several examples of the defect, and the whole visual field may not be involved. Koenig's observations make it probable that this type also is dichromatic, two suitably chosen simple lights matching the whole spectrum. Blue blindness may be a reduction form, since all normal matches appear to be valid for such an eye. The neutral point is in the yellow between 566 $\mu\mu$ and 570 $\mu\mu$; the "Fehlpunkt" is close to the violet. Our knowledge of this condition is not sufficiently exact for it to be profitably discussed in a text-book.[1]

The experimental production of a form of colour-blindness by Burch has so direct a bearing on the theories of

[1] The curious reader will find sufficient references to the literature of Blue Blindness in my article on "Theories of Colour Vision" in *Further Advances in Physiology*, edited by Leonard Hill, London, 1909 (Arnold).

colour vision, that I shall consider his work in the chapter devoted to the theories of the subject. We shall next turn our attention to the phenomena of successive induction or after-images.

APPENDIX TO CHAPTER XV.

Proof of the existence of a "Fehlpunkt." [1]

Suppose the quantity r of a colour situated at R in the diagram matches the quantity g of a colour at G,

$$r = nr + (1-n)r.$$

But the quantity nr of $\mathrm{R} = ng$ of G.

Therefore if n be a proper fraction, r of R matches $(1-n)r$ of $\mathrm{R} + ng$ of G. The situation of this mixture is S

$$\text{if} \qquad \frac{\mathrm{RS}}{\mathrm{SG}} = \frac{ng}{(1-n)r} \quad . \quad . \quad . \quad (1)$$

and the quantity s of the mixed colour obtained $= ng + (1-n)r$, and this is independent of n.

If, now, we mix b parts of some other colour B with s of S, we obtain a mixed colour whose appearance is independent of n. Let its measure be t and its situation T,

$$t = b + s = b + ng + (1-n)r, \text{ and, as before, } \frac{\mathrm{TS}}{\mathrm{BT}} = \frac{b}{ng + (1-n)r} \quad . \quad . \quad . \quad (1a)$$

Draw BH perpendicular to RG and TL perpendicular to BH. Call LH, x, BH, h, TL, y, HG a, and RG c.

$$\frac{x}{h} = \frac{\mathrm{LH}}{\mathrm{BH}} = \frac{\mathrm{TS}}{\mathrm{BS}} \text{ (by similar triangles)} = \frac{b}{b + ng + (1-n)r} \; . \; . \; . \; (1)b$$

$$\frac{y}{h-x} = \frac{\mathrm{TL}}{\mathrm{BL}} = \frac{\mathrm{SH}}{\mathrm{BH}} = \frac{\mathrm{SG} - a}{h}.$$

But, from (1) $\mathrm{SG} = c\dfrac{(1-n)r}{ng + (1-n)r}$,

$$\therefore \frac{y}{h-x} = \frac{(c-a)(1-n)r - ang}{h[ng + (1-n)r]} \; . \; . \; . \; (1c)$$

Eliminating n between ($1b$) and ($1c$), we have

$$0 = ybh(g-r) - x[crg + br(c-a) + abg] + bh[(c-a)r + ag] \quad . \quad . \quad . \quad (1d)$$

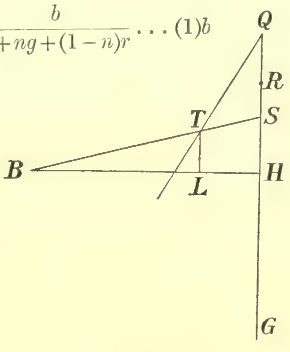


FIG. 21.

This is a linear relation between the co-ordinates x and y of T with respect to an origin H.

Therefore the locus of T is a straight line.

[1] Helmholtz, *op. cit.*, pp. 363, etc.

Let TQ be the locus intersecting RG in Q. QH $=y$ when $x=0$,

$$\therefore \quad y_0=\frac{(c-a)r+ag}{r-g},$$

i.e. is independent of b, the amount mixed from B.

Therefore all lines of equal mixtures from RGB intersect at the same point Q, or they are parallel, in which case $r=g$, and y_0 is infinite.

The distance of Q from R is given by

$$y_0-c+a=\frac{cg}{r-g}=\text{QR} \quad . \quad . \quad . \quad (1f)$$

If we mix q of the colour Q with g of the colour G, so that R results

$$\frac{\text{QR}}{\text{RG}}=\frac{g}{q}, \text{ but RG}=c,$$

$$\therefore \quad \frac{g}{r-g}=\frac{g}{q}. \quad \therefore q=r-g. \quad \therefore r=g+q.$$

Since, by hypothesis, $r=g$ and $q=r-g$ is not necessarily $=0$, the colour Q has no stimulus value for a colour-blind eye.

RECOMMENDED FOR FURTHER STUDY

The literature of Colour Blindness is enormous, and most of the papers mingle a description of experimental or clinical observations with theoretical discussions. I should advise the student first to read:—

J. von Kries, Ueber Farbensysteme, Z.P.P.S.O., vol. xiii. pp. 241–324. Having mastered this, he might read the account in Helmholtz's Handbuch, and then the more recent controversial papers.

A complete bibliography of the literature up to 1896 is appended to the second edition of Helmholtz's Handbuch. Dr. Edridge Green's work on Colour Blindness and Colour Perception, in the International Scientific Series (Kegan Paul), contains many ingenious speculations and matter of practical interest, but should be read in a critical spirit.

CHAPTER XVI

AFTER-IMAGES OR SUCCESSIVE INDUCTION

THAT after the withdrawal of a stimulus some sensation process persists has long been known. In 1634 Peiresc described the positive and negative after-images of the window, and a few years later Bonacursius maintained in opposition to the learned Jesuit Athanasius Kircher that one could see as well in the dark as by daylight, convincing his opponent by the following experiment. Kircher was taken into a room and made to look fixedly at a drawing covering a window slit; the room was then completely darkened, and Kircher once more perceived the drawing on looking at a piece of white paper in his hand. The Jesuit's own explanation of the result was that light absorbed by the eye streamed out in the dark and illuminated the paper. Similar experiments were described by Mariotte in 1668, and Newton was familiar with the phenomena, which he held to be of psychological origin. In the eighteenth century many workers observed these after-images or "accidental colours," particularly the negative or complementary images, which, as we shall find, are more easily studied. Writing in 1734, Jurin observed that the "contrary sensation is apt to arise in us, sometimes of itself, and sometimes from such causes as at another time would not produce the sensation at all, or at least not to the same degree."[1]

Scherfer (1761) investigated complementary images, and in copying a picture painted it with a green face shaded with yellow, white hair and eyebrows, black eyeballs with white pupils, and green lips, so that the after-image had the colours of the original. Robert Waring Darwin (1786) studied both positive and negative after-images, explaining clearly enough the experimental precautions essential for their demonstra-

[1] Quoted by Burch, *Proc. Roy. Soc.*, 1900, lxvi. 204.

tion, *e.g.* the necessity of excluding any extraneous light if the "direct spectrum" (positive after-image) is to be seen. Goethe in his *Farbenlehre*, which appeared in 1810, records several observations of negative after-images, of which the following is an amusing example:—

"I had entered an inn towards evening, and as a well-favoured girl with a brilliantly fair complexion, black hair, and a scarlet bodice came into the room, I looked attentively at her as she stood before me at some distance in half shadow. As she presently afterwards turned away, I saw on the white wall, which was now before me, a black face surrounded with a bright light, while the dress of the perfectly distinct figure appeared of a beautiful sea-green."[1]

During the nineteenth century the subject has been closely examined by an array of workers, amongst whom Brewster, Fechner, Brücke, Helmholtz, and Hering are, perhaps, the most prominent. I shall give a short account of the facts, avoiding, so far as possible, any theoretical pre-suppositions.

No special apparatus is required for the demonstration of some fundamental results. If one looks fixedly for 20 to 40 seconds at a moderately illuminated white spot or source of light and then shuts the eyes or looks towards a sheet of white paper, a black spot usually surrounded by a bright halo is visible. If the object be coloured, then performing a similar experiment we see a spot tinged with the complementary of the original impression. These are the negative or complementary after-images with which all are familiar.

To obtain an after-sensation identical in character with that experienced during the original stimulation, a positive after-image, somewhat greater care is necessary, since eye or body movements rapidly cause its disappearance or inhibit its production. "After waiting a sufficient time with carefully covered eyes, one turns the eyes (still covered by the hands) toward the object, taking care to remain quite still, then takes the hands away rapidly, and with the same speed brings them back again. This movement of the hands must

[1] Goethe's *Theory of Colours*, Eastlake's trans., 1840, p. 22.

be executed gently, without violent exertion or shaking of the body. If the experiment has been properly carried out, the positive after-image seen behind the covering hands is sometimes so sharply defined and bright, that it seems as though the hands were transparent and one still saw the real object. One has sufficient time to note details in the after-image which there was no time to study during the actual exposure."[1]

The first thing to grasp is that no discontinuity appears to exist between positive and negative after-images. Suppose one develops an after-image by looking at a bright object, and that on closing the eyes one obtains a bright image on a dark ground, *i.e.* a positive after-image; then if instead of closing the eyes after performing such an experiment one looks at a moderately illuminated field, a dark image on a bright ground is seen, *i.e.* a negative after-image. Between these termini we can obtain a continuous series of intermediates; for instance, we can choose a field of brightness such that, on fixating it, no after-image is obtained at all. This amounts to saying that the nature of an after-image is in the main determined by two factors: (1) The quality and intensity of the first or primarily exciting stimulus; (2) the character of the secondary or, as we may call it, modifying stimulus. In any after-image sensation, *both* factors are necessarily involved; even when the retina is shielded from external stimuli, a stimulation process is active, bound up with the sensation called by some the light chaos, by others the autocthonous retinal light. Naturally, this is not an exhaustive enumeration of the modifying factors; the conditions noted are necessary, but not sufficient. Individual peculiarities, both psychological and physiological, are involved, but our first study must be directed to the constant factors which give us a definite point of departure. Let us divide the experiments into two chief groups: (1) The eye is exposed to one extrinsic stimulus only; (2) two extrinsic stimuli are successively employed.

In (1) we have the primary stimulus compounded with

[1] Helmholtz, *Handb. d. Phys. Optik.*, second edition, p. 504.

the intrinsic retinal factor alone, in (2) the state of affairs is more complex. Before applying a stimulus, the entoptic sensation or "light chaos" is indeterminate in character, varying like most subjective phenomena with the observer. Helmholtz speaks of "manifold light points in motion often like convoluted vessels or scattered moss fibres and leaves." The appearance is often like that of waves passing slowly across the field of vision. If we regard fixedly a moderately bright object for 40 seconds and then darken the eyes, we see in the light chaos a dark patch surrounded by a bright halo: that is to say, the effect is much the same as noticed if one looks at a moderately bright surface, the "light chaos" behaves like such a surface.

Turning to the more important case (2), we find a complex of results. Let us call the first extrinsic stimulus the RETUNING LIGHT, the second extrinsic stimulus applied to the same area the REACTING LIGHT. The effect produced by the reacting light will depend on the change induced by the retuner, and can be measured by comparing its effect with that obtained on stimulating regions not exposed to the retuning light: the stimulus applied to such an area may be termed the COMPARISON LIGHT. The whole process is conveniently named RETUNING.

I have already made it seem probable that stimulus values are not the same in different parts of the retina, and that light-dark adaptation is selective; hence, that our results may be pure, we must work with small directly fixated fields and under conditions of constant adaptation, preferably light adaptation.

The first question that arises is as to the validity of the mixing laws. We can match a homogeneous yellow with a red-green mixture; if we retune with a homogeneous yellow, a reacting yellow does not, of course, match a comparison yellow, and similarly for a retuning and reacting mixture. The question is whether the responses to the two originally equal stimuli are changed to a like extent, whether the simple and mixed colours still match. Apparently the answer must be affirmative.

"On small directly fixated fields optical equations suffer

no alteration if the tuning of this part of the retina be altered by means of any light stimulus whatever. For instance, a homogeneous yellow and a centrally equivalent red-green mixture appear after previous yellow illumination both paler, after previous blue illumination both more saturated yellow, but they still match perfectly. In the same way, the equality of unanalysed daylight and a white formed by a complementary mixture is not destroyed if both fields, by means of previous colour stimulation, are strongly tinged by the complementary of the retuning light."[1]

This very important result has not escaped criticism; we are all agreed that it cannot be obtained by stimulating the peripheral region of the retina. The correctness of the experiments so far as the fovea centralis is concerned is testified to by Bühler, who has re-investigated the matter and can be provisionally accepted.

Accepting the persistence of optical equations as an experimental fact, conclusions may be drawn which enable us to deduce some interesting formulæ. Thus we can obtain a relation between the change in appearance of different reacting lights and any specified retuning. Put briefly, we may say that the change in appearance of a light as a result of retuning consists in a lowered or heightened responsiveness of the eye to that light. If R be the stimulus measure, the sensation result will depend on a product of the form $a \cdot R$, where a is a measure of the retinal excitability for R, a value dependent on the tuning; in determining the effect produced in any given case of retuning, we have only to consider the value of a. Suppose we have two retinal points A and B differently tuned, and R_1 falling on A matches R_2 at B, S_1 at A similarly matching S_2 at B. Hence (adopting the ordinary convention as to equality), $R_1 + S_1 = R_2 + S_2$.

Now let A and B be retuned by exposure to light of stimulus value T, which alters the excitability for S_1 and S_2 respectively. We now have at A, $R_1 + aS_1$, and for B, $R_2 + aS_2$, *i.e.* $R_1 + S_1 - (1-a)S_1$, and $R_2 + S_2 - (1-a)S_2$, which must match, since by hypothesis S_1 at A is equal to S_2 at B. This is the

[1] V. Kries, Nagel's *Handb.*, iii. p. 210.

essence of the so-called "Law of Coefficients," and is a short way of stating the experimental facts mentioned above. The law obviously fails in the case of feeble stimuli, because then the autocthonous stimulus (the light chaos) becomes measurable relatively to S_1, S_2, and T, and can no longer be neglected, as in the above expressions. Let us next examine some matters of detail.

First, what happens when the retuning and reacting lights are identical? This merely requires for answer a study of the sensation changes accompanying prolonged fixation of any object, and we all know the answer. Brightness differences grow smaller and smaller, being at length effaced, which suggests a relationship between the degree of retuning and the strength of the stimulus.

Next, suppose we retune as before with white, but use a chromatic reactor. We find (under conditions of light adaptation) that the reactor must have the same qualitative composition as the comparison, but greater intensity. V. Kries in his experiments obtained a good match if the amounts of coloured light in reactor and comparison were approximately in the ratio of 3 or 4 to 1. With a colour mixer, the blue sectors were 270° : 97°; the red, 270° : 84°; the yellow, 270° : 97°. If the coloured sectors were made equal, and the white so chosen that the discs were approximately equal in brightness, the sensation excited in the retuned area was always that of far too low saturation. White retuning, therefore, seems to change chromatic stimulus values; but the experiments upon which this conclusion is based have been adversely criticised by Hering, whose objections will be considered in a later chapter, when we come to deal with the theoretical side of the question.

The next case is that of retuning with a colour, and here also the simplest example is when retuner and reactor are the same. Without a comparison, loss in brightness and saturation are apparent; with a comparison, a difference in colour tone may also be perceptible. Voeste's results are as follows: A yellow (560 $\mu\mu$), a green (500 $\mu\mu$), and a blue (460 $\mu\mu$) undergo no change in hue on pro-

longed fixation; intermediates pass away from the green towards the red or the blue. Thus a light between 500 and 460 $\mu\mu$ will match a comparison of less wave length than itself; one between 500 and 560 $\mu\mu$, a light of greater wave length.

If we use a grey field as reactor it produces a sensation closely allied to that normally associated with the retuner's complementary, and this is not a mere blend of the sensation obtained in the darkened eye after retuning plus the whiteness normally excited by a grey field. If this were so, after retuning with a given yellow the subjective blue could always be compensated by mixing the same amount of yellow with the reacting field so that it might appear colourless. As a matter of fact, however, the more white there is in the reacting field, the more yellow must be mixed with it—as we should expect from the coefficient rule. If the reactor be grey, the complementary of the retuner may be very well marked; if the reactor be the complementary itself, a sensation of colour is produced far exceeding in purity that associated with any region of the spectrum; this result is universally admitted to be of considerable theoretical importance, as we shall find later. Finally, if some colour not complementary to the retuner be used as reactor various sensations are experienced, although in general the complementary of the retuner predominates. After red retuning, v. Kries matched a reacting yellow (589 $\mu\mu$) with a green-yellow (556 $\mu\mu$); after green retuning, it matched an orange (605 $\mu\mu$). Hess, after blue retuning, matched a reacting 517 $\mu\mu$ with a comparison 565 $\mu\mu$. These experiments are interesting, but a systematic study of the effects of retuning when each spectral colour is used in turn as a reactor, *with a comparison field*, has yet to be effected, and we cannot at present lay down any general laws.

The time relations of the process of retuning are of some interest. Many researches have been published, the technique of some being simple, of others elaborate. One plan is easy; a white object on a dark ground is fixated, and one ascertains, after a definite interval, what comparison

light placed near the object matches it at the moment of observation. The table contains v. Kries' results. By a similar method, we can measure the rate at which the effect passes off with a definite amount of retuning. Unfortunately, the difficulty of avoiding two important sources of error—adaptation and extra-foveal stimulation—is great, and we can lay but little stress on the results. For instance, it is not known whether the effect of retuning passes off smoothly, as Fechner and Helmholtz believed, or in pulses,

Changes in White Value (v. Kries).

Strength of Stimulus (Arbitrary Units).	Apparent Diminution After						
	Seconds.						
	3	6	10	20	40	80	160
1	·91	·81	·66	·58	·43	·23	·15
1·95	·86	·74	·62	·52	·32	·18	·09
3·9	·82	·71	·62	·34	·21	·14	·08
34·7	·74	·57	·42	·25	·16	·08	·03

as held by Aubert. It is likely that some of Aubert's evidence is vitiated by imperfect technique, but his hypothesis cannot be disproved.

Exner attempted to measure the change in sensation from the moment at which the stimulus is applied by an ingenious method, which has been used in a modified form by Burch. This method depends on the fact that with a given stimulus the sensation increases to a maximum, then, in consequence of retuning, diminishes. At a definite instant a stimulus, *e g.* a bright semicircle in a dark field, is applied; then after a known short interval a bright field is exhibited; finally, after another known interval a dark field appears. In this way two neighbouring points have the same stimulus applied to them, but on one the stimulus begins to act a fraction of a second earlier than on the other. If the first stimulus

effect has reached its maximum but the second has not, the resultant after-image will be positive; if both have passed their maxima, the after-image of the semicircle will be negative, because the first excitation process will have fallen to a lower level than the second. Between these extremes we have a point at which no differentiation appears, the field seeming to be uniform. This latter result will be obtained when one stimulus has just passed, the second just fallen short of its maximum, and accordingly gives a measure of the time necessary to attain the first maximum.

Ingenious as are these experiments, their value as measures of the time relations in retuning is not, perhaps, very great.

Evidently they depend on the assumption that sensational intensity changes after the stimulus has been withdrawn, just as it does while the stimulus is still acting. Our study of recurrent vision, particularly the brightness relations of the tertiary image, has taught us that this assumption is of doubtful truth. We thus know but little of the excitation changes quantitatively, and even from the qualitative standpoint our information is not complete. The colour changes undergone by the after-image of a colourless object generally form a white-red-green-red-blue cycle. The image of a coloured object passes from positive to negative (complementary) through a colourless or reddish-white phase. It is quite certain that the duration of after-image effects is much longer than has been generally thought. Burch passed from an ordinary into a completely darkened room and noted the sensations experienced with the following results:—

"0·5 mins.[1] Confused after-images of portions of objects recently looked at. These images gradually fade and give place to a luminous fog, made up of what I have called dazzle tints, *i.e.* coloured impressions of luminosity without form.

"10–15 mins. Fog no longer uniform but 'spotty,' with patches of a brownish or greenish-bronze colour.

"18–21 mins. A group of yellow or green luminous points.

[1] G. J. Burch, *Proc. Roy. Soc.*, B., 1905, pp. 212–213.

"23–28 mins. Green dazzle tints predominate, beginning to break up, in some cases, into patches of green showing a fainter blue between. . . .

"106–120 mins. Gradually a luminous fog seems to fill the surrounding space. For a minute or two it increases in brightness, and then breaks up near the middle in two or three places and seems to roll away on all sides. Then it returns, and again breaks up, generally leaving an island about the size of the yellow spot, which lasts two or three seconds longer than the rest. The colour of these clouds is a rich pure violet, like that of the calcium lines H and K in the arc spectrum. This phenomenon may go on from ten minutes to half-an-hour, the violet patches getting smaller and appearing at longer intervals till they die away."

To sit patiently in a dark room studying the time relations of after-images may seem crude and uninteresting to those who associate experimental research with expensive apparatus, and cannot be made to realise that some of the most brilliant achievements of physiology have been effected with the help of little except ability. It is probable that much-needed light will be thrown on the process of retuning by an extension of work, such as that of Burch. A series of experiments must be carried out, the eye being exposed for a definite time to a given light before each period of observation and the resultant changes are compared. In some such fashion we may be able to unravel the complicated tangle of results already mentioned.

Summing up the definitely ascertained conclusions, we find:—

(1) The distinction between positive and negative after-images is not absolute but relative, depending on the nature of the reacting stimulus.

(2) An image-producing or returning stimulus changes the stimulus value of a reacting (subsequently applied) light, but only in such a way that the sensation-response following exposure to the reacting light is increased or diminished quantitatively. Colour equations do not lose their validity.

(3) The latter statement, as expressed in the "Coefficient

Law," is true in the case of foveal vision, but not for peripheral stimulation.

(4) We do not know the time relations of the retuning process, nor whether the latter proceeds uniformly or in pulses.

I have now reviewed briefly the chief experimental data upon which a theory of visual sensations (exclusive of spatial perceptions) must rest. The question of simultaneous contrast has indeed been omitted, but owing to certain peculiarities of this branch of the subject it is best postponed until the more generally interesting theories of colour vision have been examined. We shall therefore now pass on to the theoretical side of our investigation, and endeavour to co-ordinate the apparently heterogeneous facts in some logical manner. We shall see that, wide as are the apparent differences of opinion, and many as are the difficulties to be encountered, both the main theories embody something of interest and importance. It will add to the clearness of our discussion if a preliminary chapter is devoted to some ancient theories of vision, and these will be examined in the following pages.

BOOKS AND PAPERS RECOMMENDED FOR FURTHER STUDY

Helmholtz, Hand. d. Physiol. Optik., second edition, pp. 501, etc.

V. Kries, Nagel's Handb., vol. iii. pp. 205, etc.

Tschermak, Ueber das Verhältnis von Gegenfarbe, Kompensationsfarbe und Kontrastfarbe (Pflüg. Arch., 1907, cxvii. 204).

Goethe's Farbenlehre, Eastlake's trans.

F. Klein, Nachbilder, Uebersicht und Nomenklatur (Engelmann's Arch. f. Physiol., 1908, Supp. Bd. p. 219).

G. J. Burch, Proc. Roy. Soc., 1900, lxvi. 204.

CHAPTER XVII

HISTORICAL THEORIES OF VISION

In attempting to estimate the scientific value of ancient theories of vision, it is necessary to bear in mind certain limitations which were imposed by incomplete means of investigation. Even with modern apparatus it is not easy to obtain a precise knowledge of the elaborate structures contained in the eye, hence workers unprovided with the simplest microscope knew almost nothing of facts which form part of the mental equipment of every educated man in our own time. Roughly, we may say that all the early theories agree in regarding the "pupil" of the eye and the "image" within it as of primary importance. Again, the flash of light seen on pressing or rapidly moving the eye was held to prove the existence of an inherent or native "fire," also of great significance. Thirdly, the presence of a watery substance within the eye required some explanation. The problem, as it presented itself to the earliest writers, was to assign their proper shares in the visual act to the "fire," the "image," and the "water." As knowledge of psychology or physiological psychology progressed, the theories became more intricate, and it is possible to distinguish between theories of physiological optics, theories of colour vision, and more general inquiries as to the nature of perception in general and spatial perception in particular. Work under the last heading is much the most subtle, and has proved of enduring interest and value for modern thinkers. The speculations as to anatomy and physiological optics are, for the reasons above recited, of little importance; while the theories of colour vision occupy an intermediate place, having in some respects proved fruitful, in others barren. As any one who is familiar with the subject will recognise, it is not in all cases easy to separate out an author's theory of vision into the sections enumerated,

and my account of the matter will not be so clear as I could wish. I shall try in this chapter to outline the main theories of vision, especially in regard to colour vision; purely anatomical or physical theories will not be examined.

One of the earliest Greek writers on this subject was Alcmæon of Cretona (fl. 500 B.C.), but our knowledge of his opinions is fragmentary. He appears to have thought that seeing is accomplished by the passage of rays from the ocular "fire" to the object, and that these returning to the eye, altered in some way, are reflected in the diaphanous "water." The fire is therefore the active element in vision. It is not clear how Alcmæon harmonised the conception of a visual ray from the "fire" with that of mirroring in the "water."

Empedocles (*circa* 450 B.C.) evolved a more subtle theory, but it is not easy to reconcile different statements attributed to him. According to the first doctrine enunciated by Empedocles, *like perceives like.* All bodies are characterised by the following properties: (1) All are made up of four elements—earth, air, fire, and water. (2) All are permeated by minute passages or pores, and all give off emanations which enter the pores. Thus, in perception, emanations from the object pass into the pores of the percipient organ. But that this passage may be effected it is necessary that the emanations and the pores should correspond; if the former be too large or too small for the latter, no perception can occur. Hence with the eye alone can we perceive emanations of colour, because these are "symmetrical" with the pores of the eye alone. This correspondence is the basis of sense specificity. Further, there is a symmetrical arrangement within the eye itself with respect to the different forms of stimulation. By means of the intra-ocular fire we perceive the emanations of fire—*i.e.* white; with the water we see water—*i.e.* black; and so on. "With earth we see earth, with water we see water, with air we see the bright air; just as with love we (perceive) love, and with hate, baleful hate."[1] Empedocles is said to have regarded four colours—white, black, red, and green—as primaries (Stobæus), but only

[1] Beare, *Greek Theories of Elementary Cognition from Alcmæon to Aristotle*, p. 18.

examines black and white in detail. He also taught that rays issued from the visual "fire," but how he associated this with his general doctrine of pores and emanations is not clear. It is probable, judging from some passages in Lucretius' great poem,[1] that a somewhat similar doctrine was held by Epicurus.

Democritus (? 460–357 B.C.) agreed with Empedocles in postulating the entrance of particles from an object into pores contained in the perceiving structure, and in the dictum that "like is perceived by like." But he denied that there were four qualitatively distinct elements, believing that all things were made up of homogeneous atoms moving in a vacuum and infinitely numerous. Vision is due to the mirroring of an object in the eye, the latter's character being somehow determined by its moist and porous nature. This part of Democritus' theory was sharply criticised by Aristotle, who remarked, "It is absurd that it should not have occurred to him to doubt why the eye alone sees, but nothing else in which energies are apparent. That the sight is aqueous is true; yet it does not happen that it sees because it is aqueous, but because it is diaphanous, which is also common to air."[2]

Democritus seems to have been the first writer to attempt a detailed theory of colours, the simple ones being white, black, red, and green. White is the smooth, because anything which is not rough, does not throw shadows, and is not difficult to penetrate, is bright. Black consists of atomic figures of an opposite kind, viz. those which are rough, uneven, and dissimilar: on this account they cast shadows, and their pores are neither straight nor easily permeable. Red is formed of the same kind of atomic figures as the hot, but the figures of red are larger. A proof that red is composed of such atoms as those forming hot is, that "we ourselves are red when heated, just as other things are when ignited, as long as they continue to have the character of 'the igneous'; but ignited things are redder in proportion as they are formed of large figures, such as flame, coals, or

[1] Lucr., *De Rer. Nat.*, ii. 833.

[2] Aristotle, *De Sensu et Sensilibus*, Taylor's trans., vol. iii. 133.

wood, whether green or dry, and also iron and other metals which are subject to ignition."[1] Green is formed of the solid and the void, the tint varying with their position and arrangement. Each colour is purer the more the figures of which it is essentially composed are free from admixture with others. All other colours are mixtures of these four. For instance, purple is mixed from white, black, and red, red being in largest and black in smallest amount. Owing to white coming midway, the colour is pleasant to the sense.

It is hardly possible for us to criticise this theory with understanding. Here, as so often in considering ancient science, one is conscious of the gulf which separates us from the world which has passed away. Much which seems meaningless or nonsensical probably only does so because not only has the author's work come down to us in a fragmentary state, but it is impossible to see things from his point of view, or even to find out what that point of view was. In ancient times, Theophrastus, who no doubt understood it better than we do, criticised Democritus' theory in so far as it deals with colour. He says that Democritus made a difficulty by suggesting four primaries rather than two—black and white—and objects that the position of the atoms rather than their shape or figure should be the cause of colour. The matter is, however, so obscure, that it can hardly be pursued in this place.

The views of Anaxagoras (499–428 B.C.) and of Diogenes of Appolonia (fifth century B.C.) can, for similar reasons, be passed over rapidly. Anaxagoras held, in opposition to his contemporaries, although the opposition is more formal than real, that perception is the result, not of like operating on like, but of the reaction between contrary and contrary. The "image" is not reflected upon a part of like colour to the object, but upon a different colour.

Diogenes, who believed that an all-pervading air was the ultimate agency in nature, has left no distinct theory of colour vision.

We now come to one of the great names in scientific history, that of Plato, whose views, although far less

[1] Beare, *op. cit.*, p. 32.

suggestive than those of Aristotle, are well worth consideration.

Plato has considered the problem from two different points of view. His account of the physical side of the matter, as one may term it, is contained in a passage in the *Timæus*, of which the following quotation gives an idea:—

"And of the organs they first contrived the eyes to give light, fixing them by a cause on this wise. They contrived that as much of fire as would not have the power of burning, but would only give a gentle light, the light of everyday life, should be formed into a body; and the pure fire which is within us and akin to this they made to flow through the eyes in a single entire and smooth substance, at the same time compressing the centre of the eye so as to retain all the grosser element, and only to allow this to be sifted through pure. When therefore the light of day surrounds the stream of vision, then like falls upon like, and there is a union, and one body is formed by natural affinity according to the direction of the eyes, wherever the light that falls from within meets that which comes from an external body. And everything being affected by likeness, whatever touches or is touched by the stream of vision, their motions are diffused over the whole body and reach the soul, producing that perception which we call sight."[1]

In the genesis of colour, particles are discharged from external things and impinge upon the eye, some being larger, some smaller, and some equal in magnitude to the parts of the eye. All colours are compounded of four—white, black, bright, and red. Bright when mixed with red and white becomes golden-yellow; red blended with black and white yields violet.

From statements in the *Timæus* and *Republic* it would seem that Plato, unlike Democritus, believed in the objective existence of colour, but, as Helmholtz pointed out, his views seem to have varied. In the *Theætetus*, colour is considered from a different standpoint, as will be clear from the next quotation: "We shall see that every colour, white, black, and every other colour, arises out of the eye meeting

[1] Plato, *Timæus*, Jowett's trans., ii. 375.

the appropriate motion, and that what we term the substance of each colour is neither the active nor the passive element, but something which passes between them and is peculiar to each percipient. . . .

"When the eye and the appropriate object meet together and give birth to whiteness, and the sensation of whiteness which could not have been given by either of them going to any other object; while the sight is flowing from the eye, and whiteness from the colour-producing element, the eye becomes fulfilled with sight and sees, and becomes not sight, but a seeing eye; the object which combines in forming the colour is fulfilled with whiteness and becomes not whiteness, but white."[1]

It may be said that Plato's views are interesting, but do not embody any complete theory of colour vision.

Aristotle (384–322 B.C.) elaborated a theory which is not the least important of his contributions to natural knowledge and, clothed in modern notation, still survives.

According to Aristotle, the *object* of sight is colour. Colour is at the surface of all visible bodies, but in order to be seen requires the presence of light, which is the medium of vision. This basal proposition formed part of the teaching of Epicurus, to judge from a notable passage in the work of his greatest exponent,[2] but in developing the conception Aristotle far surpassed Epicurus.

Light, says Aristotle, presupposes a diaphanous substrate, which in its turn is the medium of light. Examples of this "diaphanous" are air, water, and many solids. The realisation or actualisation of this potential quality of being diaphanous is light, its absence darkness. When the former condition of actual light is established in the diaphanous medium, any coloured body sets up a movement in it between object and eye; this is the essential process in colour perception. The diaphanous substrate upon which depends the existence of light and, *a fortiori*, colour is not peculiar to the bodies called transparent or diaphanous, but is a species of universally diffused natural power; it is not indeed

[1] Plato, *Theætetus*, Jowett's trans., vol. iii. 538–9.

[2] Lucretius, *De Rerum Nat.*, ii. 730–833, especially 795–8.

capable of existence independently of "body," but subsists in varying degrees in all things. The colour of a body either forms its surface or is upon its surface, the latter opinion being the more exact since the indeterminate "diaphanous" of air and water exhibits colour, which, however, owing to the indeterminate boundary, is variable. This explains the changing hues of sea and sky.

Bodies with a definite boundary have a fixed colour, so that one might again define colour as the surface limit of the diaphanous in determinately bounded body. This definition is consistent with the first given, viz. that which stimulates the actualised "diaphanous" (light) between the object and the eye, but the latter is a definition in terms of vision and the medium of vision, the former in terms of the object as it exists apart from vision.

Colour is a genus comprising seven species; it is a quality, and cannot therefore exist without a substrate. The seven species are white, black, golden-yellow, crimson, violet, leek-green, and deep blue. The colour genus (like all other genera of sensible qualities) consists of species lying between extremes; outside these extremes there can be no colours, between them are specific boundaries. By subdividing the scale limited by the extremes, we cannot obtain an infinite number of distinct colours, because a sensible quality is discrete, not continuous. By dividing the substrate we do not arrive at any new colour; the halves of a white object are white. It is true that by sufficiently fine division no colour whatever may be perceptible, but on reuniting these portions we again obtain white. The two limits are black and white; when one is *actually* existent, the other is *potentially* existent. The transition from white to black is effected through the successive degrees, which are the species of colour. The substratum, of which these are the qualities, is one, and is in strictness that which is changed; the colours alternate.

Colour is not purely subjective; it is true that it depends upon the eye, but it also depends upon the object. Actual colour depends upon the possibilities of these two being realised together, but the coloured object existed in nature

as a potential colour before the act of vision, and apart from it. "It is light that at once transforms the potential colour to actuality, and the potentially seeing to an actually seeing eye."[1]

In the colour scale (as among the elements) there is a sort of opposition of positive and negative. White is the positive, black the negative. This is Aristotle's general doctrine of colours; he also treats certain of them in detail.

The presence of some fire-like element is the cause of light in the diaphanous, and in its absence we have darkness. In all determinately bounded bodies we may assume something analogous with the presence and absence of this fiery element. Its absence means blackness, its presence whiteness. Therefore, in determinately bounded bodies, blackness is privation of whiteness. Blackness and whiteness are contraries within one sensory province, that of colour, and from them all the other colours are to be explained. "The transition from white to black is possible through continuous degrees of privation; that from white to black is likewise possible by an ascending scale in the opposite direction. The various colours are species which fall between the two contraries, and are generated of certain combinations of these."[2] For instance, in passing from white to black we first come to crimson. As the intervening stages in the passage mark relative extremes, change can start from any point.

With regard to the actual mode of origin of the intermediate colours, what is actually effected in the abovementioned process? Aristotle's views on this point are not quite consistent in his different writings, but he appears to condemn the doctrine of atomic juxtaposition and that of superposition, taking the view that a complete blending occurs; by blending is meant a compound or mixture of so intimate a nature that no individual part retains its original qualities unmodified.

The colour spoken of as grey is sometimes described as standing at the mid-point of the scale between black and white, sometimes as a sort of relative black. Golden-yellow is also nearly akin to white. Red is produced by

[1] Beare, *op. cit.*, p. 64. [2] *Ibid.*, p. 69.

light streaming through black, as when the sun shines through a fog. Purple is akin to crimson, but differs from it in having more of the dark constituent. "Sometimes the light of a lamp shows not white but purple, the ray that is sent from it being feeble, and being reflected from a dark colour. This increasing feebleness of the ray brings us from purple to *leek-green* and *violet* successively. The stronger ray yields *crimson* against the dark ground (or when mixed with dark); the next in strength gives *leek-green*; the weakest, *violet*."[1]

In this connection, Aristotle refers to positive and negative after-images. After looking at the sun and closing the eyes we see the object first of the same colour as before; this changes to crimson, then to purple, then to black, and finally vanishes. The order illustrates the genesis of colours from the blending of white and black. Simultaneous contrast receives an explanation along these lines—the brightest rainbow is seen in the darkest cloud, white wool has its colour intensified when placed next black wool, etc. Aristotle rejected altogether the theory of emanations and pores, while his conception of a vibratile movement imparted to the actualised "diaphanous" may, perhaps, be regarded as a partial anticipation of the modern doctrine of a luminiferous æther. We cannot, however, push the comparison far, since he maintained, in opposition to Empedocles, that light does not travel.

The eye itself is like other organs to be defined in terms of its function, and thus is an eye only so long as it can see. The eye of a corpse is so called only in a somewhat incorrect way. The eye is the organ which is stimulated by colour, but this process of stimulation must in some way be transmitted to the "soul." It seems to follow that the diaphanous medium which acts objectively is also functioning within the eye itself in order to transmit the stimulation inwards. The eye consists of heterogeneous parts; that part which is specially concerned in vision is the part generally translated pupil, but probably, at least after the time of Empedocles, meaning rather the crystalline

[1] Beare, *op. cit.*, p. 75.

lens. Surrounding this internal moist part comes what Aristotle terms the black (? iris), and outside of this again is the white (? sclerotic). The pupil and vision are to the eye what body and soul are respectively in the whole living creature.[1]

For perfect vision there must be a proper amount of moisture in the eye. Those creatures which have too little see well by night but ill by day, because owing to the deficiency the eyes are over-stimulated by daylight. The other group, with too much moisture, can see well by daylight but badly in the night, because there is not relatively to the water enough fire in the eye. The membrane which covers the "pupil" must be transparent, white, thin, and smooth.

Aristotle rejects the theory that the eye consists of fire, a theory which, as we have noticed, rests on the observation of phosphenes (flashes of light seen when the eye is rapidly moved or when it is pressed). If, asks Aristotle, the eye is igneous, why do we not always see these phosphenes, instead of only under exceptional circumstances? Further, why does not the eye see itself always? Besides, if the visual part of the eye were really fire, we ought to be able to see in the dark, and Plato's explanation of the circumstance that we cannot see in the dark, viz. an extinction of the visual ray in the darkness, is inadmissible. Such fire as is made with coals may indeed be extinguished by cold and moisture, but not light.

The previous pages will be sufficient to give the reader some idea of the nature of Greek thought respecting the visual processes. A few general remarks may fittingly conclude the chapter.

For the reasons mentioned at the beginning, the statements respecting the anatomical and physical side of the problem of sight are of little interest. It cannot be said that even Aristotle's view of the matter is particularly helpful. It will have been noticed how the dogma of like producing like hampered work on this side, already sufficiently difficult, and the value of Müller's doctrine (*vide supra*,

[1] See Beare, *op. cit.*, p. 80.

Chapter I.) receives a practical illustration. Since the external medium is transparent, there must be some internal transparency; since "fire" is visible, there must be some internal "fire" by which it is perceived, and so on. Anaxagoras might appear to be an exception, but a little thought convinces one that the exception is only formal. In adopting the converse of the dogma, like produces like, he too stands committed to the belief that there is some necessary connection *in kind* between the processes occurring within us and those conceptually existent outside of us.

The theories of vision as a problem in physiological psychology, on the other hand, stand on quite a different plane. As we shall see in the chapter on Hering's theory of visual sensations, Aristotle's teaching was the basis of Goethe's theory of colours, and the doctrine of Goethe, freed from certain mathematico-physical absurdities, partly a result of imperfect physical knowledge, has been transformed by Hering into a hypothesis of rare ingenuity and intellectual value.

To pursue the history of visual theories from the Greek period to the modern epoch would be of little more than antiquarian interest. In another chapter I shall refer to the work of Berkeley in connection with the theory of space; his contribution to the theory of colour vision in the strict sense is not of much importance from the physiological standpoint.

RECOMMENDED FOR FURTHER STUDY

There is a considerable literature dealing with the sense physiology and psychology of the ancients, but it is mainly written from the standpoint of the psychologist or that of the philologist. The reader will find ample material for extending his knowledge in the work of Professor Beare, to which I have frequently called attention. Jowett's translation of Plato's Dialogues can be profitably consulted for the earlier speculations. The standard work on Aristotle is *Aristotles ueber die Farben*, von C. Prant, München, 1849.

CHAPTER XVIII

THE YOUNG-HELMHOLTZ THEORY OF COLOUR VISION

As I attempted to show in the chapter on normal vision, Newton's researches demonstrating the (conceptually) complex nature of white light and the physical substratum of chromatic stimuli—as co-ordinated by the undulatory hypothesis—enable us to form a coherent, but not necessarily, or even probably final, account of the physical elements involved in retinal stimulation. On the other hand, the specificity of physiological response, which finds a not quite accurate expression in Müller's law, releases us from many of the difficulties attendant upon the primitive theories of vision, the propounders of which were hampered by the dogma of physico-physiological identity. The acceptance of these facts has left wide scope for ingenuity in the construction of theories as to the psycho-physiological mechanism which links together the subjective and objective visual worlds; but the liberty of choice which is thus accorded to the scientific imagination has its own disadvantages. Perhaps the most obvious is the impossibility in which we stand of "proving"—in the more popular sense of that much abused word—any theory of colour vision to be true or false. So long as it was held that a conceptual system of physics was a valid physiological and psychological system, that our physiological categories were to be tested against our physical classifications, it was comparatively easy to judge and condemn a theory of vision. We now hold that the writ of the physical court does not run in the kingdom of physiology, and we do not know to what jurisdiction a physiological theory of colour vision is amenable. This is one of the reasons, in fact the chief reason, why an enormous number of rival theories are in the field, and why their study has seemed to

many highly educated men as unprofitable as the mediæval disputes of the schoolmen. To those who have the leisure, and the particular form of intellectual curiosity which is attracted to the study of human ingenuity divorced from the immediate phenomena of nature, a complete history of modern theories of vision would be instructive and valuable; but by those whose leisure is less ample, and whose curiosity does not take this form, a different path must be followed. One must consider the theories of vision which, it may be, rather from the energy of their propounders than from any overwhelming speculative merit in the theories themselves, have borne the most fruit in respect of experimental observations and methods. Adopting this criterion, two theories stand out above the rest, those of Helmholtz and Hering. If, therefore, these theories only are discussed in the present work, it is not because I hold them to be necessarily superior as theories to others—for instance, those of Ladd-Franklin and Schenck—but because they have borne so much more experimental fruit. In a famous passage, R. L. Stevenson describes a conversation. "What I advance," said one, "is true." "Yes," replied the other, "but not the whole truth." "Sir," was the retort, "there is no such thing as the whole truth." In what follows, the reader should have that aphorism constantly in his mind.

In attempting to arrive at an adequate interpretation of any class of experimental facts, it is permissible to advance by more than one route, just as many problems in geometry can be solved by analytical as by pure geometrical methods. As a rule, it does not much matter which path we choose, so long as we keep count of any assumptions made and avoid the introduction of unnecessary steps. We shall now start from the experimental laws of colour mixing and see whither we arrive by following the most obvious route. We found that for most experimental purposes, we could say that a sensation "produced by" a colour stimulus could be matched by a sensation due to a stimulus obtained by mixing not more than three lights together. We saw that these three lights did not coincide accurately with any spectral colours, but that if we admitted negative values into our colour

equations, our vision could be regarded as definitely trichromatic even in terms of known stimuli. In order, however, to avoid this, let us so choose our stimuli that only positive values of each are employed. This means that they must be so chosen that the colour "triangle" is circumscribed by the lines joining their representative points in a plane, *e.g.*

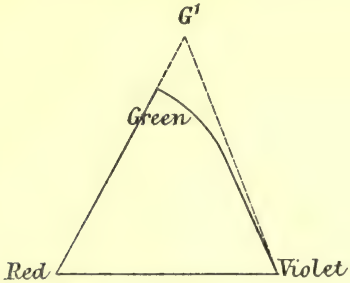


FIG. 22.

This is our first assumption, and is little more than a generalisation of experimental facts.

Thus far, we have merely asserted that a stimulus R′, say, can be expressed by the equation $R' = x.R + y.G + z.V$, where x, y, z are real positive quantities. But our only measure of equality of stimulation being corresponding equality of sensations, we imply (and this is our second and most important assumption) that there is a definite relationship between the physiological excitatory processes which lead up to sensations and the stimulus magnitudes.

This assumption is justified if we can show that it leads to the formulation of a useful working hypothesis, and if we assume the simplest relationship consistent with the experimental facts. What, then, is the simplest relation we can suppose to subsist between the stimulatory and excitatory processes? Clearly that just as stimuli may be reduced to terms of three independent variables, excitatory processes are represented by three independent variables. Thus, taking our previous example, any stimulus $R' = x.R + y.G + z.V$, then $A = f_1(x, y, z)$, $B = f_2(x, y, z)$, $C = f_3(x, y, z)$, and conversely, $x = F_1(A, B, C)$, $y = F_2(A, B, C)$, $z = F_3(A, B, C)$.

These latter expressions may be taken as "elements" or unit excitatory processes, or any linear function of them may be so taken.[1]

The conception is merely that three independent physiological processes exist, each of which is defined by a functional equation connecting it with the three independent stimulus values which, as we have seen, measure the effect of any given stimulus.

This statement contains the fundamental part of the hypothesis first sketched by Thomas Young and elaborated by Helmholtz. It is important to distinguish the essentials of the theory from its subsidiary parts.

The effect produced by any chromatic stimulus is supposed to depend upon changes set up in three independent "substances," nothing being postulated with respect to them except that the magnitude of change in each is a function, *i.e.* depends on the proportions of three independently variable stimuli in terms of which the given stimulus can be expressed. Conversely, any given stimulus value is a function of the independent activities of three visual "substances." The nature of the "substances" from a physiological point of view, also the exact relations between them and the stimuli, are left undiscussed. For convenience of illustration, Young and Helmholtz assumed that the activity of each substance was associated with a single colour sensation, and chose red, green, and violet as "elementary sensations" from the present standpoint. "Substance" A, when stimulated, was supposed to give rise to the sensation of red; B, under similar conditions, to that of green; and C, to that of violet or violet-blue; in this way the well-known "valency curves" of the text-books were obtained. The advantage of this method is that the theory seems more definite, but the disadvantage is entailed that if the illustration proves irreconcilable with facts of experiment, the reader omits to notice that what is found wanting is merely an illustration, not the basal theory. It is especially important to remember that the colour operations discussed in Chapter XIV. do not pretend to describe any

[1] For a proof of this statement, see Helmholtz, *Handb. d. Physiol. Opt.*, second edition, pp. 342-3. The section beginning on p. 341 should be closely studied.

direct relation between the hypothetical "substances" and stimulus magnitudes.

In precisely the same way, for the sake of illustration, Helmholtz suggested the existence somewhere in the retino-cerebral apparatus of three sets of fibres, each corresponding to one of the hypothetical "substances." This suggestion was less happy because its utility was not so great as, and the chance of misunderstanding greater than, in the previous case. The red, green, and violet fibres have been persistently misunderstood; it is time to remember that they are pure abstractions, no more essential to the theory just sketched than is the employment in algebra of the letter x to denote an unknown quantity an essential procedure in that science. To avoid this fertile source of misunderstanding I shall use Professor v. Kries' term, Components, and speak of the theory as the "Three Components Hypothesis."

Another mistake is illustrated by the following quotation from a paper by Miss Calkins:[1]—

"From the point of view of a psychological analysis of our conscious sensations of colour, the postulates of this theory are not in accordance with the facts of observation; for, even granting that violet is a simple fundamental colour sensation (which many observers regard as complex), it can hardly be denied that yellow is just as well characterised and definite a sensation as red or green. Yellow looks yellow, and does not seem at all like a mixture of red and green, or indeed any other colour mixture."

Objections of this type are, I think, irrelevant. The theory is only an attempt to express physiological processes in terms of experimental facts, *i.e.* of stimulus values; it has nothing to do with the psychological analysis of sensations. Whether such an analysis can be performed is a question which must be decided by psychologists, it is no part of our inquiry. We are only concerned with sensations in so far as they are the signs of the existence of physiological changes.

Having reduced the hypothesis to its simplest terms, let

[1] *Arch. f. Physiologie*, Supp. Vol., 1902, pp. 244 *et seq.*

us apply it to the facts resumed in earlier chapters. That it describes normal visual systems is, of course, apparent, since they form its starting point. Abnormal trichromatic systems are satisfactorily described if we suppose one of the visual components to be defined in a peculiar way. Thus, if a component A is normally defined as $f_1(x, y, z)$, in these cases it is some other function, $f_1'(x, y, z)$, say, of the stimulus values.

Turning to dichromatic systems, we have seen that, from the experimental standpoint, they are reduction forms of a normal system. Theoretically, the simplest reduction we could imagine would be the absence or ineffectiveness of one of the three normal components. Thus if we take R, G, V (for the sake of clearness) as the normal components, in the absence of R all sensations (sensation being used with the meaning above defined) are functions of G and V only, a condition *approximating* to that of protanopes. If G be absent and R present, we get a form resembling deuteranopia.

Under such conditions, not only would the relation between dichromatics and trichromatics be easily intelligible, but we could determine from observations on dichromatics the components of a normal system, or, more precisely, the stimuli which act exclusively upon such components. A stimulus inoperative upon a dichromatic eye must act exclusively upon the missing component. We have learned (Chapter XV.) how to find the position of such a stimulus in the colour triangle (the "Fehlpunkt"), and the two such points obtained for the two systems of dichromatic vision determine the stimulus relations of two visual components in the normal eye.

All this depends, however, on the assumption that one component is absent and everything else unchanged in a dichromatic eye. Modern work renders it more than doubtful whether we may make this assumption. In 1885, when the second edition of his classical treatise was being prepared, Helmholtz wrote as follows to Lord Rayleigh: "I have never doubted that our colour system depended on three variables, and no more. In regard to colour-

blindness, the recent observations of Donders and of my assistant, Dr. A. Koenig, show that this defect cannot be referred simply to the lack of one of the fundamental colours, but that two of the primaries (red and green) appear to acquire a more even distribution in the spectrum, so that now one and now the other makes a more vigorous impression; in other words, the resulting curve approximates now more to the red and now to the green sensation. In addition to this we have every shade of lessened power of discrimination. Consequently different individuals require very different mixtures of lithium and thallium light in order to make up sodium light." [1]

But if we cannot regard dichromatic vision as differing from the normal merely in the absence of a component, we can, in terms of the fundamental hypothesis, assert that it depends upon a visual system made up of two variables defined by such expressions as $A' = F_1 (x, y, z)$ and $B' = F_2 (x, y, z)$. This way of looking at the matter, although consistent and logical enough, is not free from objection. We could not deduce from such expressions any definite statements respecting the components of normal systems; the description is too general to admit of detailed verification. To put the matter in a nutshell, the older conception of partial colour-blindness as due to the absence of one normal component is simple and, if true, practical, but is not, in fact, quite adequate; the more general statement is adequate, but not very helpful. Next, what has the Three Components Hypothesis to say with regard to the phenomena of after-images?

A noteworthy feature of after-image experiments is, of course, that stimulation with a given light increases responsiveness to its complementary. It would appear, therefore, easy to imagine that activity of the three components, or any one or two of them, in a certain way diminishes their responsiveness in one direction, increasing it in another direction. This amounts to supposing that we have a condition comparable with the state of the reflex arcs, so brilliantly described by Sherrington; the nervous path is

[1] Rolingsberger's *Life of Helmholtz*, English trans., Oxford, 1907, p. 436.

occupied by one form of motor discharge, and this very occupancy paves the way for a discharge different, and even opposite, in kind.

To so highly general a statement as this no objection will be found, but if we investigate details, difficulties arise. For instance, the apparent saturation of spectral colours is greatly enhanced by previously stimulating the eye with their complementaries. Helmholtz accordingly supposed that all the spectral colours act on each visual component. But if this be true, the simpler interpretation of colour-blindness once more fails. Observations of dichromatics suggest that lights having wave lengths greater than 550 $\mu\mu$ do not affect the third component (the "blue" or "violet") at all, because no standard blue had to be mixed with the standard red in order to effect a good match with colours in this part of the spectrum. To a normal eye, however, the saturation of spectral yellow (589 $\mu\mu$) is unquestionably enhanced by previous exposure to blue. Either spectral colours do not affect all three components, in which case the theory does not cover after-image effects, or the simpler explanation of partial colour-blindness must be abandoned. In view of what has already been said, the reader will perhaps agree that the second alternative is the more plausible, and conclude that after-images are adequately described at the cost of strengthening our suspicion that dichromatic and trichromatic systems cannot be co-ordinated in any simple manner.

So far we have found that the Hypothesis of Three Components describes with sufficient clearness the facts of normal colour vision, including the phenomena of after-images; that it also describes the facts of partial colour-blindness, but in very general terms, the earlier direct explanation being insufficient. We have next to see whether any experimental evidence can be found pointing to the existence of independent visual components satisfying the conditions of the theory or conceivably capable of so satisfying them.

Evidence of this kind has been afforded by the experiments of G. J. Burch. This observer exposed his eye to direct sunlight in the focus of a 2-inch lens behind coloured

glasses. A gelatine film stained with magenta and combined with a medium ruby glass was found to transmit a fairly pure red, three thicknesses of green glass were used for green, and a tank of cupric ammonia-sulphate for violet. Similar arrangements were made for the other hues, and in some experiments a large spectroscope was employed. Two minutes' exposure was sufficient to produce the maximal effect in the case of red. After exposure to red light, the following effects were noticed. Scarlet geraniums appeared black, calceolarias and sunflowers green, purple flowers, such as clematis, violet. Pink roses were sky-blue. Fatiguing with violet light caused objects reflecting violet light to appear black, purples and reds seemed crimson. Green stimulation made the foliage appear reddish or bluish-grey. After these exposures, "the colour by which the eye has been dazzled, and to which it is now blind, tint all those objects which naturally reflect none of this." This statement is illustrated by a simple experiment of Burch's. Suppose the eye to be somewhat fatigued by green, as during a long summer walk in the country, if the eye be directed to a small red spot on a black surface, *e.g.* a geranium petal on the black cover of a book, and one walks quickly with it into a dark shed or barn, the colour of the petal changes from red through orange and yellow, becoming eventually, perhaps, whitish. On coming into the light again the red reappears.

These interesting experiments suggest that stimulation with red, green, and violet alters responsiveness with respect to these stimuli alone, and the same is the case with blue. Orange stimulation, on the other hand, affects not only the appearance of the orange, but that of the red and the green as well. Both positive and negative effects pass off rapidly in the case of artificial red-blindness (in ten minutes), more slowly after violet fatigue (in two hours).

It is, I think, obvious that the state of affairs presented by these experiments is highly complex. We are dealing with a change in responsiveness analogous to the retuning effects of Chapter XVI., but of greater magnitude and in less simple form. Take the experiment quoted as to the

apparent hue of a geranium petal after green stimulation; this is an ordinary after-image effect, and differs in no way from the results obtained by other workers; in the case of exposure to stronger green light, the effect is similar. How does this, we may ask, differ from the experiment with intense orange light? Simply in the fact that "retuning" with orange affects responsiveness to red and green as well, so that they, like orange itself, will cause the production of negative after-images. The conclusion that in this case the mechanism involved in the production of orange is compounded of a mechanism yielding a sensation of redness and a mechanism responding with a sensation of greenness is reasonable, and finds confirmation in a recent experiment performed by Burch.

We know that responsiveness to green is increased, relatively to that for red stimulation, by resting the eye in darkness: hence if orange or yellow depends upon a fusion of two physiological processes, one concerned with green, the other with red, then, under conditions of feeble illumination and dark adaptation, the yellow should appear greenish, because the mechanism responding by a sensation of greenness is more active under these conditions than that associated in the same way with redness. One speaks of a physiological process responding by the production of a sensation purely for brevity; it is not psychologically accurate, but the psychological reader is not likely to be misled. Burch found the result to be as expected—"the sodium lines appeared pale green when of the minimum visible intensity."

These results do, therefore, support a contention that components in the sense of our theory may possibly have a physiological counterpart. I do not think, however, that the view that four components—a red, a green, a violet, and a blue—exist is proved by Burch's experiments, valuable though these are. To prove that any light acts upon only one component it would be necessary to show that after dazzling with, *e.g.*, blue, any mixed light was altered by the subtraction of blue, and that any light not containing blue had that colour added to it. The facts that the condition is

transitory is perhaps attended with some risk, and almost certainly involves psychological complications, render exact observations difficult. Under the circumstances it is perhaps best to say that although the experiments are perfectly consistent with a component hypothesis of the type discussed, it would be rash, on the strength of them, to make any general statement as to the nature of the components from the physiological standpoint. Theoretically, it does not matter whether we adopt three or four components; the algebraical form of our theory would not be changed, but we should lose the practical advantages of considering normal colour vision to be, experimentally, trichromatic, which would be a serious objection.

Before finally summarising the case presented, two matters need attention. First, as to monochromatic vision or total colour-blindness. It has been asserted that such a condition cannot be described in terms of the Young-Helmholtz theory. As a matter of fact, the assertion is inaccurate; symbolically we could cover the facts by supposing that the functions defining the variables are identical, thus: $A = f_1(x, y, z) = B = f_2(x, y, z) = C = f_3(x, y, z)$, or graphically we can put it that the three valency curves coincide. In any case, the reader will have probably seen reason to think that monochromatic vision depends upon a mechanism entirely distinct from the precursors of normal foveal vision, and that its treatment should be kept separate from that of the phenomena with which we are here concerned.

In the second place, no reference has been made to Simultaneous Contrast. The reason is, that it seems doubtful whether the phenomena of simultaneous contrast are not of quite a special kind. It is true that the original hypothesis of Helmholtz, which assumed that contrastive effects are dependent upon factors purely psychological in nature, can hardly be maintained without some modification, but I shall reserve a discussion of the point for a later chapter. It must be said, however, that if subsequent work should compel us to assign a *purely* physiological basis to the facts of simultaneous contrast, it will probably be necessary to modify the theory of components in such a way that it will become some-

what more complicated than it is at present. Leaving this matter for further consideration, we can say that the component hypothesis associated with the names of Young and Helmholtz supposes (1) that colour sensations depend upon the activity of three independent physiological substances of unknown nature and situation; (2) that the relationship between these components and the complex of stimuli is expressible quantitatively by saying that the responsiveness of each component is measured by a real linear function of three standard stimuli; (3) the results of stimulating these components are unit sensations in *a purely physiological sense*, not units of consciousness; (4) no spectral light acts upon only one of the components.

The theory describes with sufficient accuracy the main facts, and there is some direct experimental evidence—that of Burch—which is consistent with its truth. The main objection to the hypothesis in its modern form is its highly general nature and want of direct applicability to the immediate data of physiological and physical research. How far this is a real objection may be a matter of discussion, but it at least inclines one to examine those theories which are, in the colloquial phrase, less up in the clouds. Such an examination will be the object of our next chapter.

RECOMMENDED FOR FURTHER STUDY

Helmholtz's treatise should, of course, be the first work consulted. The reader should then turn to v. Kries' article in Nagel's Handb. The following papers of Burch describe his experiments:—

(1) Phil. Trans., B., vol. cxci. pp. 1-34.

(2) Proc. Roy. Soc., vol. lxvi. pp. 216–219.

(3) Proc. Roy. Soc., B., 1905, p. 214.

CHAPTER XIX

HERING'S THEORY OF VISUAL SENSATIONS

In the last chapter I attempted to trace out the theoretical consequences developed by Young and Helmholtz from the experimental facts of colour-mixing. It will have been clear that the whole web of deductions depended from the fact that, in general, the effect of a given stimulus or combination of stimuli was constant, so that we might attribute to the stimulus a causal value. In other words, we have regarded the sensations of colour as *signs* or *differentiæ* of processes initiated by the stimuli; the resulting theory was accordingly not in any real sense a theory of visual sensations, but one of visual stimuli.

If the estimate I formed of the value of this process be in any measure just, it would seem to follow that its weakness lay rather in what was left unsaid than in any positive error. One cannot but notice in the theory as at present advanced a certain dryness, a detachment from one's experience of colour on the subjective side, which is repellent. All this possibly amounts to saying that the theory is not very simple nor very direct, objections which can be urged against many theories of wider intellectual value than that of Young and Helmholtz in other fields of thought, objections which are not by any means fatal. Recognising the existence of these difficulties, however, it is well to see whether we can obtain a more satisfactory solution of our problem by approaching it in a somewhat different way. This chapter will be devoted to the study of another proposed solution of the matter, that of Ewald Hering.

This other line of investigation practically resumes the problem at the point at which the Greeks left it, and dates from the publication in 1810 of Goethe's *Farbenlehre.* The comparatively slight direct influence of this work on the develop-

ment of modern physiological thought respecting the nature of physiological processes is due to causes well worthy of attention. The physical analysis of white light into monochromatic constituents by Newton had naturally attracted the chief, almost the exclusive, attention of those who occupied themselves with the study of colour vision. Goethe, however, with characteristic intellectual insight saw that the difficulties of the problem were not to be overcome by vague references to physical experiments. He saw that the problem was one of sensations, and he approached it from the sensational standpoint. Had he contented himself with this, with an analysis of sensations of colour, his work must have had an enormous influence; but he went further. The prevailing tendency to over-estimate the significance of the physical side of the question led Goethe into the opposite error. He sustained the thesis that the Newtonian analysis was physically incorrect, and that the alleged decomposition of white light was not in general possible. Consequently, much of his work is devoted to an attack upon the Newtonian doctrine from the physical side, an attack which signally failed. Unfortunately the failure of this attack involved more valuable parts of Goethe's work in discredit, and his book is not well known even to professional physiologists. I can best give an idea of the valuable parts by quoting a few passages which are specially relevant for us.

"With regard to the German terminology, it has the advantage of possessing four monosyllabic names no longer to be traced to their origin, viz. yellow (*Gelb*), blue, red, green. They represent the most general idea of colour to the imagination, without reference to any very specific modification. If we were to add two other qualifying terms to each of these four, as thus, red-yellow and yellow-red, red-blue and blue-red, yellow-green and green-yellow, blue-green and green-blue, we should express the gradations of the chromatic circle with sufficient distinctness; and if we were to add the designations of light and dark, and again define, in some measure, the degree of purity or its opposite by the monosyllables black, white, grey, brown, we should have a tolerably sufficient range of expressions to

describe the ordinary appearances presented to us, without troubling ourselves whether they were produced dynamically or atomically."[1]

"Considered in a general point of view, colour is determined towards one of two sides. It thus presents a contrast which we call a polarity, and which we may fitly designate by the expressions *plus* and *minus*.

Plus.	Minus.
Yellow.	Blue.
Action.	Negation.
Light.	Shadow.
Brightness.	Darkness.
Force.	Weakness.
Warmth.	Coldness.
Proximity.	Distance.
Repulsion.	Attraction.
Affinity with acids.	Affinity with alkalis."[2]

We see here formulated the conception of certain colour sensations as occupying unique places in our sensational field, and presenting also, as it were, a species of sensational contrast one with another.

Of course in many respects this idea is an old one, and has perhaps always been realised by painters. In a dialogue on colours by Ludovico Dolce, published in 1565, the following passage occurs: "He who wishes to combine colours that are agreeable to the eye will put grey next dusky orange, yellow-green next rose colour, blue next orange, dark purple, black, next dark green, white next black, and white next flesh colour."[3]

Titian, according to his biographer Ridolfi, was fond of opposing red and blue to his flesh tints, and Rubens contrasted a bright red with his "still cooler flesh colour" (Eastlake).

Here, as elsewhere, the greatest art is to conceal the art. A study of the works of Rembrandt, whose skill in contrastive effects has never been equalled, reveals the fact that

[1] Goethe's *Theory of Colours*, Eastlake's translation, London, 1840, pp. 243-4.

[2] Goethe, *op. cit.*, p. 276.

[3] *Ibid.*, Note C.

the most striking effects are produced by light-dark contrasts rather than specific colour oppositions. The remarkable specific brightness (*vide infra*) of yellow is, however, well seen in the (so-called) "Nachtwache"; the extraordinarily vivid effect produced by the yellow dress of one of the central figures is balanced by general shadow, without, so far as I could judge, any obvious use of the "Gegenfarbe." These remarks seem to me to apply also to the "Staalmeesters." I hope that some day a physiologist with a competent knowledge of art will undertake a study of the master works of art from the standpoint of the physiology of vision.

The point to mark in the preceding passages is the general agreement that certain of our sensations of colour are really singled out from the whole group as presenting sharply defined, special characters. All sensational theories are primarily concerned with the definition of these characters, and secondarily with an attempt to describe the data in terms of a physiological hypothesis. Of such attempts the views developed by Professor Ewald Hering of Leipzig and his pupils during the last five-and-thirty years are the most valuable results. Whatever may be our ultimate conclusion as to the validity of these theories, no one can doubt that they have greatly advanced our knowledge of visual physiology, and their study cannot be neglected by any one desirous of acquiring even a superficial idea of modern conceptions. Whenever I come upon a new writer dealing with colour vision, I turn to his account of Hering's theories; if he dismisses them as "obviously" incorrect or absurd, I am confident that his own contribution to the subject is a very small one.

According to Hering's method of analysis, our whole visual world can be resolved into six elementary qualities of sensation; white, black, the toneless, and blue, yellow, green, red, the toned or bright (*bunte*) colours. If one considers the tone-free qualities, they can be arranged to form a series of shades or gradations passing from the intensest white to the deepest black. If one attends to the toned colours, they can be arranged in a circle with four divisions.

"If we choose in such a colour circle any colour as starting

point—for instance, a red similar to that with which a spectrum usually begins at the long-waved end—we see the red colours arranged in one direction gradually becoming more yellowish, while the redness of the colours correspondingly diminishes, until finally, passing through orange and golden-yellow, we arrive at a yellow which contains no trace of the red which is still so apparent in the orange. To this yellow succeed other yellow colours which play more and more into the green (sulphur-yellow, canary-yellow); further on (as in sap-green) the yellowishness recedes more and more behind the steadily increasing greenishness, until we finally reach a green which seems to be entirely free from yellow. To this succeed green colours which already play into blue (water-green); further on the bluishness of the colours becomes increasingly stronger, the greenishness weaker, until we finally reach a blue exhibiting no more greenishness at all. To this blue succeed blue colours of increasing reddishness and correspondingly diminishing bluishness (blue-violet, red-violet, purple-red), until the last trace of bluishness vanishes in a definite red."[1]

If we define a pure green as a sensation free from admixture with that of blue and yellow, and the other three sensation qualities in the same manner, we see that our pure colours (from this point of view) can be arranged in two pairs, yellow and blue forming one, and red and green the other. The members of each pair can be placed opposite one another in a diagram, because we can only pass from yellow to blue or from red to green by traversing the province of a member of the other pair, as just explained. There is no pure yellowish-blue or reddish-green sensation quality.

But there is yet another contrast, from the standpoint of sensation quality, between yellow and red on the one hand, and blue and green on the other. Somehow, in a manner difficult to express in words, yet of universal experience, the two former colours are associated with a certain heightening and increased vividness of sensation tone. This finds its ex-

[1] Ewald Hering, *Gründzüge der Lehre vom Lichtsinn*, Leipzig, 1905, p. 41.

pression in the classification by artists of colour into warm and cold. Goethe has emphasised these points:—

"We find from experience again that yellow excites a warm and agreeable impression. Hence in painting it belongs to the illumined and emphatic side.

"This impression of warmth may be experienced in a very lively and emphatic manner if we look at a landscape through a yellow glass, particularly on a grey winter's day. The eye is gladdened, the heart expanded and cheered, a glow seems at once to breathe towards us."[1]

Of blue he says: "This colour has a peculiar and almost indescribable effect upon the eye. As a hue it is powerful, but it is on the negative side, and in its highest purity is, as it were, a stimulating negation. Its appearance, then, is a kind of contradiction between excitement and repose.

"Rooms which are hung with pure blue appear in some degree larger, but at the same time empty and cold.

"The appearance of objects seen through a blue glass is gloomy and melancholy."[2]

In the opinion of Hering, the facts are most satisfactorily described by saying that in the sensation-complex blue and green produce a darkening and yellow or red a brightening effect; the toneless colours, black and white, also contribute respectively in a negative or positive sense to the sum-total of effects. We have, therefore, the brightness of a colour defined in strictly sensational terms.

We have now reached the conception of six primary sensation qualities arranged in three pairs—white-red, red-green, yellow-blue. The first member in each case increases, the second diminishes the subjective intensity or brightness of a sensation complex of which it forms part.[3]

"The brightness or darkness of a toned (*bunte*) colour is, according to this view, the result of the inherent brightness or darkness (*Eigenhell und Eigendunkel*) of its constituent pure colours, which as the pure constituents of that colour agreeably to their respective distinctness determine

[1] Goethe, *op. cit.*, p. 307. [2] *Ibid.*, p. 310.

[3] Sensation-complex is a term used merely to indicate the supposed multiplicity of infra-conscious representatives, not in reference to perception.

the quality of the colour. In any colour really existent for us is a definite inherent degree of brightness and darkness, and in accordance with whether the brightness or the darkness be the more distinct, we call the colour bright or dark.

"A toned colour may generally be regarded as made up of four primary components, two toned and two tone-free (black and white). Only in colours of the tone of a pure colour is one toned constituent present by itself. In any red-yellow colour, *e.g.* orange, we have accordingly to distinguish three bright, pure components (red, yellow, white), and one dark (black); but in any green-blue, three dark (green, blue, black) and one bright. The red-green and green-yellow colours would contain, however, two bright and two dark pure components.

"From what has been said, the following rules can be deduced:—

"If two colours of equal tone and equal purity differ in brightness, this is due to a difference in their black-white components.

"Two colours differing in tone may, notwithstanding equal degrees of purity and equality as regards their black-white components, differ in brightness.

"With equality of conditions as to the black-white components, a yellow, a red, or a yellow-red colour is so much the brighter, a blue, a green, or a blue-green so much the darker the more distinct the colour tone in comparison with the black-white constituent." [1]

This quotation describes what is often called the theory of the "Specific Brightness of Colours." The whole is, or claims to be, a faithful analysis of our visual sensations without reference to any hypothesis whatever. That this is a perfectly legitimate process I have already attempted to show; the next step is to translate these facts, or supposed facts, into terms of a physiological hypothesis. Such a translation can be readily effected.

It is supposed that somewhere in the retino-cerebral apparatus, in the infra-conscious sphere, four distinct sub-

[1] Hering, *op. cit.*, p. 61.

stances exist. Each of these substances can undergo a building up, or anabolic, and a breaking down, or katabolic, change. External stimuli will, depending on their natures, induce either an anabolic or a katabolic change in these substances, and are associated with definite sensations of colour. The building up of the black-white substance corresponds to a sensation of blackness, its breaking down to a sensation of whiteness; anabolism of the red-green substance is associated with green colouration, its katabolism with red colouration; similarly in the third substance yellow is katabolic in origin, blue anabolic.

Before discussing these views in detail, I must warn the reader against some popular misconceptions. Certain opponents have asserted or suggested that the facts upon which Hering founded his theory differ in some perverse way from those data which are ordinarily called facts of experiment. This is not the case. The facts the hypothesis attempts to describe are as legitimately objects of inquiry as any others within the purview of physiological science. It is further to be noted that the four physiological "substances" have just as much and just as little real existence as the three components of our other theory. It is idle to say that the postulated anabolic and katabolic processes are essentially unlike any chemical mechanisms with which we are acquainted. It is equally vain to object that stimulation processes in animate nature are to all appearance bound up with katabolic changes; this would only be a valid objection if we attempted to identify the hypothetical substances with any known retino-cerebral constituent. No such identification is attempted; the suggestion that Hering and his school identify the black-white substance with visual purple is entirely unjustified. The fact is, that this theory can only be judged on the grounds of scientific expediency. Does Hering's method give us a better account of the phenomena of colour vision than that based upon stimulus relations? This is the only question worth the physiologist's while to answer.

One notices directly that the hypothesis, in the form in which it has just been presented, offers two considerable

advantages. Firstly, it deals with the immediate data of vision, the sensations of colour, directly, not merely in terms of stimulation magnitudes. In the second place, it is essentially easy to comprehend, which cannot, perhaps, be said of the components' hypothesis. Let us first of all attempt to express the facts of successive contrast, after-images, in terms of this hypothesis. After resting the eye on a white object we should expect, under certain conditions, a positive, under others a negative after-effect, and experiment agrees with theory. For example, if the eye be stimulated with green light, anabolism will occur in the red-green substance, an anabolism which will lead to the formation of a large quantity of "material." If, now, red light stimulates the retina it produces not only katabolism of the normal quantity of substance, but the new formed material also falls to pieces, and the correlative sensation is greatly enhanced. That a positive after-image will sometimes be produced might be expected. After the stimulus is withdrawn, the anabolic (or katabolic) change induced by it will continue for some short space of time owing to a species of chemical inertia in the substance. In fact, all the obvious phenomena of after-images are well enough described in terms of Hering's theory; it is when we come to the details that trouble arises.

It was noticed by v. Kries that the responsiveness of the eye to monochromatic light was markedly altered by previous exposure to white. He found that the stimulus value of the red he employed was diminished in the ratio of about one to four by previously retuning the eye with white. The validity of v. Kries' conclusions has been contested by Hering, who objected that the colour used by v. Kries as a reactor (180° blue, 180° white on a disc) was not sufficiently saturated, and brings forward the following experiment: Two discs, A and B, are arranged. A consists of a black centre surrounded by a white ring, B of a centre composed of 120° blue and 240° black, encircled by a ring containing 356° blue and 4° white. A point upon the internal margin of the white ring in A is fixated for a given time, and the experimenter then turns his eye to an exactly corresponding point in B. Hering always found that the outer ring of

B, under these conditions, looked more saturated than the centre.

As the term saturated is not used by Hering in the physical sense, the exact bearing of his objection to v. Kries' experiment is not clear. Presumably he holds that the "blueness" of v. Kries' disc was not distinctly separable from its "whiteness," with the result that the apparent change in the latter on retuning with white was mistaken for a change in the former. If this objection is admissible, it is to be observed that in Hering's experiment the difference between the amounts of blue in reacting and comparison fields was so great that an enormous diminution in responsiveness over the retuned area would be necessary for the production of a good match between the centre and the periphery of B. It is contended that after white retuning a reacting blue and white can be made to match a pure blue in brightness by adding more white; adding more blue will always make the reactor too saturated. Hering's experiment actually demonstrates that a diminution of some $66\frac{2}{3}$ per cent. in apparent intensity cannot be attained by retuning with the white he employed. That the apparent brightness *was* correspondingly reduced is, of course, evidence in his favour, but the difficulties of specific brightness comparison are under such conditions not small.

The conclusion of Hering's memoir is so important from the theoretical standpoint, that I quote it verbatim.

"To the change of state experienced by an element of the somatic visual field when acted upon by, *e.g.*, blue light, with which the blue sensation is associated, the whole somatic visual field reacts by a change in the opposite direction which corresponds to the oppositely coloured or yellow sensation, and any light that now falls on the retina acts, in consequence of this chromatic retuning of the visual field, as if its yellow valency were increased and its blue valency correspondingly diminished. This retuning is maximal in the immediate vicinity of the element acted upon by the blue light, and diminishes with its distance from the same. . . . A white light falling on the neighbourhood of the region which has been stimulated with blue seems therefore more

or less yellowish, but a white light which falls together with blue on the spot that has been stimulated with blue, seeing that it behaves as a more or less yellow-valent light, neutralises the blue valency of the blue light so much the more the greater be the quantity of it mixed with the latter. This explains the striking fact that the chromatic quality of a saturated colour is so extremely quickly extinguished by increasing the amount of white mixed with it. . . .

"When v. Kries, therefore, supposed that, according to the theory of opposite colours (*Gegenfarben*), the same result would be obtained from a fatigued and an unfatigued area if the same quantity of blue were allowed to fall on both, but in addition on the fatigued area a suitably chosen quantity of white light, he was in error. In such a case the blue valency of the blue light at the unfatigued area is unaltered, since no other light is mixed with it; over the fatigued area the blue valency of the blue light is partly neutralised by the admixture of white. Accordingly the blue at this latter area must appear less saturated than at the former. In fact, a transitory equality in brightness and saturation between the two areas is only obtained when white is indeed mixed with blue for the fatigued area, but, on the other hand, the blue light for the unfatigued area is suitably diminished. In general, for reasons already given, an equality in colour tone for blue can only be obtained under exceptional circumstances when the character of the daylight is specially favourable, and the tone of the blue just right."[1]

It is clear, therefore, that while white tuning is held by Hering not to affect colour valency, chromatic retuning does markedly affect white valency. In other words, what is, sensationally, a pure white has a definite colour valency; pure white, in terms of the physiological process in the white-black "substance," is hypothetical. We see again in Hering's theory the weak point we noticed in the hypothesis of Young and Helmholtz, viz. the necessity of complicating the theory in order to make it cover the facts, a necessity which brings the theory out of touch with the immediate

[1] Hering, "Ueber die von der Farbenempfindlichkeit unabhängige Aenderung der Weissempfindlichkeit," *Pflüg. Arch.*, xciv. (1903), 533.

data of experience. It is rather interesting to notice that Hering's theory becomes more difficult to follow by developing in a direction opposite to that followed by the other theory; the latter became unsatisfactory, to some, by tending to be too general, the former by multiplying its detailed sub-hypothesis.

I cannot too strongly urge on the reader the consideration that such difficulties will always arise; they are bound up with the progress of knowledge. An explanation which was satisfactory at the date of its publication ceases to be so as the volume of scientific output in the subject of which it treats widens. In this sense all theories are creatures of a day.

Hering's account of partial colour-blindness is subject to similar, but perhaps stronger, objections. He originally taught that in partial colour-blindness the red-green substance was absent. In view of the fact that there are two forms of partial colour-blindness further explanation was necessary, and a most ingenious conception, a conception which in all probability contains at least some truth, was evolved. We have seen that trichromatic systems exist which differ appreciably from the normal in responsiveness to yellow and blue light. We have also seen that pigmentation of the retina and the lens influence appreciably colour matches. Hering suggested, and supported his suggestion by some observations on subjects of the two forms of trichromatic anomaly, that the two forms of partial colour-blindness were, in a sense, extreme forms of yellow and blue sightedness combined with extremely marked or extremely slight pigmentation. The protanopes would centre round the blue anomaly (relatively blue sighted), and the deuteranopes round the yellow anomaly (relatively yellow sighted). That the conception of continuous variation in colour sense is antecedently probable must be admitted; there is much reason to think that the occurrence of discontinuous variation in biological characters is far less common than certain enthusiasts would have us believe. It must, however, be said that the observations of v. Kries and others, which were alluded to in an earlier chapter, have made it difficult for us to believe that the difference between protanopia

and deuteranopia is not more definite than this explanation would suggest. Tschermak,[1] a prominent supporter of Hering's views, seems more or less definitely to abandon this attempt to describe dichromatic vision, and, so far as I know, an adequate expression of the facts in terms of Hering's hypothesis has not yet been found.

Our general conclusions, therefore, may perhaps be expressed in the following way:—

The theory associated with the name of Hering is an attempt to arrive at a general conception of the visual processes by an analysis and comparison of sensations of colour. In this way prominence is given to many important facts neither specially nor adequately resumed in the theory founded on stimulus relations. If, however, we attempt to build up upon such data an hypothesis adequate to the task of describing *all* the experimental facts, difficulties are encountered not less formidable than those associated with the Young-Helmholtz theory.

In attempting to meet their respective difficulties the two theories became unsatisfactory in different ways. The stimulus hypothesis becomes too general, the sensational hypothesis too detailed. Examples have been seen in the former's treatment of dichromatic vision, and in the latter's account of after-images.

The most tempting reconciliation of the modes of analysis is to suppose that the theories are in some sense complementary—a view akin to that of Donders[2]—that they both contain some measure of truth, surveying the vast complex of phenomena from different points of views. Neither theory is wholly true nor yet wholly false, nor does adhesion to the one imply total rejection of its ostensible rival.

Of the numerous other theories of colour vision I do not, for reasons already given, intend to speak; many, especially perhaps those of Schenck and Ladd-Franklin,[3] are highly

[1] Tschermak, *Ergebn. d. Physiologie*, 1st Jahrg. (1902), second part, p. 795.

[2] Donders, *Archif. f. Opthalm.*, 1881, xxvii. part 1, p. 55; *ibid.*, 1884, xxx. part 1, p. 15.

[3] Schenck, *Pflüg. Arch.*, cxviii. (1907), p. 161. Ladd-Franklin, *Z.P.P.S.O.*, iv. (1893), 211.

ingenious; all contain some points of importance, but none can be compared in interest and educational value with those we have examined in the last two chapters.

RECOMMENDED FOR FURTHER STUDY

The best account in English, and written with judicial impartiality, is that of *Dr. Rivers*, Schafer's Text-book of Physiology, Edinburgh, 1900, vol. ii. p. 1026.

IN SUPPORT OF THE YOUNG-HELMHOLTZ THEORY—
Helmholtz, Handb. d. Physiol. Optik., second edition.
V. Kries, Nagel's Handb., vol. iii. p. 109.

IN SUPPORT OF HERING'S THEORY—
Hering, Gründzüge der Lehre vom Lichtsinn (Sonderabdruck a. d. Handbuch d. Augenheilkunde, 1 Teil, xii. Kap.). Leipzig, 1905–7, Engelmann. (This is an admirably clear account so far as it has gone, but the separate publication appears to be delayed.)

CHAPTER XX

SIMULTANEOUS CONTRAST

It may be regarded as a very general truth of sense physiology that the sum of the effects produced by two simultaneous stimuli is not equal to the total effect produced by two stimuli applied successively. The mutual effect exerted in this way by two synchronous excitations is revealed to us subjectively as *contrast*. Although this phenomenon of contrast is observed in each department of sensation, its study is most conveniently effected in the case of vision, and a rich harvest of results has been garnered by workers in this field. For this reason I shall confine myself to a study of visual contrast; the generalisation of the results, together with the modifications necessary in special cases, is an exercise which may profitably be left to the reader.

Although it is perfectly true that the fundamental experiments in simultaneous contrast are readily performed, the subject in its detailed examination is not free from difficulty, and a satisfactory theory has not yet been propounded. In summarising the experimental methods and results I shall follow the order adopted by Tschermak,[1] whose memoir is both lucid and exhaustive. The theoretical considerations which I shall finally submit, although not in any true sense novel, will be found to differ slightly from the usual interpretations. The first class of experiments comprises Surface or Areal Contrast, in which the alteration is appreciable over a comparatively large surface. These experiments can be subdivided again into brightness or black-white contrasts and colour contrasts.

The simplest instance in the first group is the varying brightness of a scrap of grey paper in accordance with the whiteness or blackness of the background against which it is viewed. Hering has demonstrated this in his elegant "Doppel-Zimmer" experiments. A circular aperture in an

[1] A. v. Tschermak, "Ueber Kontrast und Irradiation," *Ergebnisse d. Physiol.*, 1903, second part, pp. 726–798, with exhaustive bibliography.

opaque partition is kept constantly illuminated; its apparent brightness is, however, seen to vary with changes in its environment. Generally the two contrasting surfaces are concentric, but this is merely for convenience of experiment, as Aubert pointed out.

Areal colour contrast has long been known, the simple fact that a colour tends to produce an apparent complementary tinging of a neighbouring field having been pointed out by Leonardo da Vinci. The ordinary laboratory method of demonstration is known as Meyer's experiment, although the principle is really due to Johannes Müller. A sheet of green (for example) paper is spread out and a scrap of grey paper placed in the middle, the whole being covered with tissue paper. The grey scrap appears of a distinct rose hue. Another method depends on the colouring of an objectively colourless mirrored light or shadow which is caused by a coloured background. Goethe noticed that the image of window bars reflected from the upper surface of a piece of green glass was purple.

The best form of the experiment is due to Ragona Scina, and has been slightly modified by Hering. The observer looks through a sheet of coloured glass inclined at an angle of 45° to a horizontal sheet of paper with black and white figures on it—for instance, rings of about 1 cm. in breadth; a second sheet of white paper is placed vertically opposite the inclined plate.[1] The black rings on the horizontal sheet, upon which colourless light is mirrored by the vertical sheet, are brightly tinged by contrast. The white rings appear in the saturated and the ground in the unsaturated colour of the glass. Cobalt glass gives, I think, the best effect, but ordinary red glass does very well.

Probably the most striking effect of all is that of coloured shadows, the existence of which was recognised by Leonardo da Vinci and Otto von Guericke. For demonstration purposes no special apparatus is necessary, and I find the follow-

[1] This sheet, which should be at right angles to that seen through the glass, ought to have black and white rings on it alternating with those on the other sheet, so that the colour of the white rings seen through the glass is not weakened by mirroring of white light from corresponding rings on the vertical sheet.

ing arrangement quite good. Set up vertically on a table a large white screen, and lean against it a lecturer's pointer. Darken the room except for one window slit, which gives a sharp shadow on the screen. On the side of the table away from the window stand an ordinary electric table lamp, so that a second shadow is formed on the screen. The window shadow is diffusely illuminated by the yellow electric light, and looks yellow; the lamp shadow, which is diffusely illuminated by the window light and should appear grey, is strongly blue. The contrastive nature of the appearance is demonstrated by switching off the electric light, when the shadow at once loses its colour. The most exact application of the method is due to Hering, and is, in principle, as follows: Two parallel slits are made in a vertical shutter; one is covered with ground glass, the other with coloured glass, the double shadow being focussed on a white screen. Another good method is that of Helmholtz. A small black disc is brought upon the dividing line of a half-white, half-green field and looked at through a fragment of Iceland spar. The extraordinary image of polarisation of the green falling on the ordinary white image forms an unsaturated green middle stripe. Internal to this the ordinary image of the right side of the black disc loses its whiteness and appears saturated green; the extraordinary image of the left half of the disc also appears internal, but is illuminated with white, and appears in the contrast colour.

Another form of contrast observations relates to the changes observed at the margin of a field. For instance, a grey disc on a black ground appears brighter at the periphery than at the centre, and a white trellis work on a dark ground seems darker at the points of crossing than at other parts. This emphasis, as it were, of the margin is responsible for some of the beauties of mountain scenery, the graduation of grey values in mountain peaks with intensification of the contour lines.

We must now consider some details of the contrastive action.

(1) *The Spatial Extent of the Effect.*

The intensity of the contrast diminishes rapidly as we pass

out from the excited area, and a very slight separation of the contrasting fields makes a considerable difference in the result. A small black line separating two fields markedly diminishes the contrast, a fact to which Helmholtz attributes much importance. A somewhat important observation is that of Charpentier, that the liminal stimulus value for a given retinal area is the same whether light be completely excluded from that area or contrast blackness induced by stimulating a neighbouring point. If true, this opinion tells strongly against the theory of contrast advanced by Hering (*vide infra*), but many observations are difficult to reconcile with it, especially those of Brewster, Meyer, and Aubert.

(2) *The temporal Succession of Contrast Effects.*

The optimum contrast effect is attained after a measurable but very short period of time (Exner), and it then falls off rapidly. Hering showed "that any true contrastive effect is most marked at the beginning of the observation (apart from the very short period of development), and diminishes rapidly, only remaining distinct for a very short interval." He attributes contradictory results to the occurrence of after-images associated with movements of the eye. With long continued fixation the contrast colour fades, giving place to its complementary (Hering's Simultaneous Coloured or Colourless Induction).

By employing a colourless disc in a coloured field, when the contrast has faded, the complementary colour gradually appears, increasing in saturation until finally disc and field fuse together. Accordingly during fixation of the object itself the negative after-image may result, a sudden diminution in the amount of light being a specially favouring circumstance. It is, therefore, a difficult matter to observe accurately the time relations of simultaneous contrast with the exclusion of after-images. Absolutely steady fixation, utilisation of the first moment of appearance of the induced colour, and short duration of the whole experiment are essential conditions.

The relations between simultaneous and successive contrast were exhaustively studied in Hering's laboratory by Kuhnt. He used colourless discs on a moderately illuminated

background of coloured glass or paper. With red and green the simultaneous contrastive effect endures for some seconds, with yellow or blue the effect is but momentary. In the end, in all cases, disc and background become indistinguishable.

It is generally held that contrastive effects are better marked in indirect than in foveal vision, which naturally suggests that light-dark adaptation would be of importance in this connection. Some experiments support this conclusion, but no systematic inquiries have, I think, been published.

Quantitative Laws of Simultaneous Contrast

(1) *White-Black Contrast.*

It has been generally held that the subjective brightness of a measurably illuminated surface varies when seen against a background of varying illumination. Lehmann, as the result of numerous experiments, concluded that the maximum contrastive effect was attained when the illuminations of background and disc were in a constant ratio (about 4·76) to one another. Ebbinghaus' results were somewhat complicated. He asserted that contrastive whiteness was proportional to the difference between the intensities of illumination of the contrasting fields and independent of their absolute magnitudes.

Contrast darkening, on the other hand, was said to be proportional to the difference of the illuminations multiplied by their quotient, and accordingly depended on absolute intensity.

Hess and Pretori, who repeated the work with special precautions, agree with Ebbinghaus in respect of contrastive whiteness, but disagree with his rule for contrast darkening, which, they hold, follows the same law as was found in the opposite case.

(2) *Colour Contrast.*

This has been studied somewhat exhaustively by Pretori and Sachs in Hering's laboratory. In their first series of experiments they worked in the following way. In the contrast-exciting field they used a coloured paper and a grey paper, which looked exactly like it to a dark adapted eye.

In the contrast-suffering field (for brevity, I shall write c.e. and c.s. fields) a definite grey was used, formed by mixing black and white, while the initial contrastive tinging was sought to be eliminated by the introduction of a coloured sector. In the experiments the coloured sector in the c.e. field was continuously increased, that in the c.s. field kept constant, the contrastive tinging being obliterated by using a larger and larger black sector. They found that with a constant white valency in the c.e. field, combined with increasing colour valency, the same magnitude in colour contrastive effect is reached with a simply proportional diminution of white valency in the c.s. field.

If the c.e. light were kept constant, and the amount of white in the c.s. field increased, the amount of contrast effect rises from zero to a certain optimum amount.

In the second series of experiments the coloured sector of the c.e. field was kept constant and the grey varied. The coloured sector of the c.s. field was maintained constant and the white sector varied until the contrastive tinging disappeared. Under these conditions the optimum contrastive effect was attained with a proportionally higher white valency of the c.s. field. In the third series of observations, both coloured and colourless components of the c.e. field were varied, but in such ratio that the white valency increased at the same rate as the colour valency. In the c.s. field the white sector was varied.

In general, they found no increase in the contrastive effect when both white and coloured components of the c.e. field were thus varied (*i.e.* with a constant saturation of the colour), but some experiments indicated an increase in contrastive effect with the intensity of the c.e. field up to a definite maximum.

The Colour of the Stimulus and that of the Contrasting Field

It has long been known that, under ordinary conditions, the contrast colour is not exactly complementary to the exciting colour, and a similar, more striking, discrepancy has been observed in ordinary after-images. The fact is

undoubted, but the explanation is obscure. Since, in general, the variation takes the form of an apparent addition of blue-red to the true complementary, and is either slight or absent after prolonged dark adaptation, Hering has supposed that ordinary daylight possesses a certain (yellowish) colour valency, so that the eye is not, in his terminology, in a condition of neutral tuning. The explanation is undoubtedly ingenious, but its discussion would be out of place in an elementary work, a remark which also applies to individual and pathological anomalies in contrast effect.

Binocular Contrast

The earliest experiments on this subject were due to Smith, Brewster, Fechner, and Meyer. A white object against a dark background was binocularly viewed, and one eye was illuminated through the sclerotic with a beam of yellowish-red light. To that eye the object appeared blue-green, to the other, of the same tinge as the objective side light. The most striking demonstration of binocular contrast is probably that devised by Hering. One eye looks through a red, the other through a blue glass of not very different brightness, both glasses being sloped obliquely from the nasal to the temporal side to allow saturation to be suitably regulated by mirroring white light from side screens. A black stripe on a white ground is doubled by increasing or diminishing the ocular convergence. Although the observed background is here and there patchy, now red, now blue, owing to "retinal rivalry," or sometimes a uniform whitish-violet, the stripe seen through the red glass looks green, and the image for the eye looking through the blue glass appears yellow.

The Theories of Simultaneous Contrast

In early times much difference of opinion prevailed as to whether contrast colour was objective in nature or a subjective phenomenon, but the problem cannot be said to have attained much importance in the theory of sensory processes before the time of Helmholtz. The theory ac-

cepted by Brücke, and elaborated by Helmholtz, denies that the basis of contrast action is a physiological alteration in any of the percipient structures, and has consequently been termed a psychological theory. It must, however, be thoroughly grasped from the outset that consciousness was not thought by Helmholtz to have any part in the genesis of contrast. It is the more needful to realise this, because certain passages in the treatise of Helmholtz are so worded that it is very difficult to avoid the inference that he is invoking a process of conscious judgment to account for the facts. Some of the more superficial students of Helmholtz have undoubtedly fallen into this error. As to this, it is sufficient to remark that the experiment in Binocular Contrast just described is alone sufficient to disprove the possibility of consciousness intervening in the matter at all, since, if we make such an assumption, we should have to believe in the possibility of two incorrect judgments respecting the same objects, and inconsistent one with the other, being simultaneously entertained, which is evidently absurd. With this caution, I shall enter upon a description of the Brücke-Helmholtz theory.

The basis of pure simultaneous contrast, especially of marginal contrast, is not a change in the mechanism of sensation, but a change in our infra-conscious interpretation of the sensation. Through the continuous and predominating influence of one colour, the standard of what we call white undergoes a change. Great errors in judgment as to colour are obviated by the existence of retinal light (the sensation experienced when the eyes are closed), but if an object is viewed under circumstances which render comparison with an objective standard difficult or impossible, then errors arise. Helmholtz performed the experiment of Ragona Scina, already described in a slightly different way. Vertical and horizontal sheets of paper were white, on the vertical plate is a black, and on the horizontal a white and a black scrap of paper. The black spot is seen in the contrast colour, rose-red, when the glass plate is green. Helmholtz explains this in the following terms:—

"One judges that the black spot on the lower horizontal

sheet is rose-red, but also judges that one sees this spot with its rose-red colour like the whole sheet through the green glass, and that the green colour given by the glass extends itself without a break over the whole underlying surface, including the dark spot. One believes, therefore, that at this place one sees simultaneously two colours, viz. green, which one ascribes to the glass plate, and rose-red, which one ascribes to the paper, and both together give, as a matter of fact, the true colour of this part, namely white. In fact, an object which, when viewed through green glass, sends white light to the eye, like this spot, must be rose-red. If we now bring above the glass plate a distinctly perceived white object, there is no more reason for splitting the colour of the object in two, and it looks to us white."[1]

He describes Meyer's experiment in almost identical language:—

"It is the same when coloured surfaces are covered with tissue paper. If the underlying surface is green, the paper appears itself to be of a greenish colour. If, now, the substance of the paper extends without any visible interruption over the grey placed underneath, one thinks one sees an object shining through green paper, and such an object must necessarily be rose-red in order to give white light. But if the white part is definitely marked out, continuity with the greenish part of the surface is destroyed, and one regards it as a white object lying on that surface."[2]

Helmholtz also laid some stress on the observation of Osann, that the coloured shadow effect (see above) persisted when the shadow was looked at through a tube so that the contrasting field was not seen.

This theory and the arguments adduced in its favour have long been the object of Hering's attacks, attacks which must, I think, be regarded as successful, at any rate in the sense that the theory as outlined in the preceding quotations can hardly be maintained.

Hering demonstrated that recognition of the grey disc (in Meyer's experiment) as not forming a part of the green field does not destroy the contrast. He also pointed out that

[1] Helmholtz, *Phys. Optik.*, p. 560. [2] *Ibid.*

marking off the grey disc with a black pencil line, or using glazed paper (either of which, according to Helmholtz, diminished the contrast effect) also diminish after-images, which Helmholtz agreed to be of physiological origin. With regard to Ragona Scina's experiment, he took even stronger ground. He showed that in this experiment, as modified by himself, the effect is just as marked when the glass plate is not seen at all, or even its existence known to the observer. By rotating the glass plate and the horizontal sheet the rings can be seen at different distances, and even in reversed positions, without change in the contrast effect. Osann's observation is attributed by Hering to the disturbing influence of after-image formation. Hering accounts for simultaneous contrast on the general lines of the theory explained in a previous chapter, anabolism or katabolism in a visual substance leading to a reciprocal activity in the immediate vicinity of the excited substance. In what region this reciprocal effect is produced, Hering does not decide. It cannot be in the retina itself, because simultaneous contrast has been obtained on a complete central scotoma due to retinitis of the papulo-macular bundle (Tschermak), and many workers have obtained both colourless and colour contrast at the blind spot.

It would be a somewhat thankless task to examine this controversy in detail, but I venture to put forward for the reader's consideration the following attempt at reconciling the two theories.

No afferent impulse when it passes beyond the physiological level into what one may term the infra-conscious region is simplex, its entrance implies the simultaneous entrance of something not itself. The basis of a colour sensation, red, say, may be, perhaps must be, a unique chemico-physical change in the receiving organ, but there is at the next stage no such thing as red *per se*, only red in contrast to what is not red. Supposing, therefore, the products of, for instance, stimulation with white light and stimulation with red light pass on into the infra-conscious region we shall really have four things—red, not-red, white, not-white. Since the not-red and the not-white are, as it

were, solely infra-conscious products, they will tend to pass away from each other towards the immediate products of activity in the physiological field. There will therefore be an intensification of the opposition between the "real" red and the "real" white. The red and the white will have their mutual difference exaggerated. But if we remember Hering's analysis of the colour field—an analysis which, as the reader will remember, depends in no way upon any physiological hypothesis, but *is* the starting point of such an hypothesis—the opposite to white is black and to red is green. Hence we have presented in the infra-conscious sphere a (darkened) red and a green. In this way one can account for the facts of simultaneous contrast. Evidently the introduction of some third element, which may serve as a standard of reference, will destroy this simple opposition, and this is what appears to happen.

I think this way of looking at the facts better than that indicated in the quotations from Helmholtz, because it is hard to avoid the intervention of true consciousness when we use what looks like a rather complicated process of inference, as in his account of Meyer's experiment. Strictly speaking, all that is done is to transfer Hering's theory of reciprocal action to the infra-conscious sphere—I do not speak of sub-consciousness, because that term has a fairly precise psychological meaning, not corresponding to my idea —from the physiological level. This transference is, I think, necessary. In the first place, it is very difficult to form a clear conception of the physiological mechanism by which the reciprocal action can be supposed to be effected. In the second place, the idea of a simple colour sensation without any existent opposite sensation is—to me at least—unattainable. I can conceive of a single physiological change preceding the existence of the sensation of redness, but I cannot isolate that sensation when it comes into existence above the physiological level. The existence of redness seems to me to imply necessarily the simultaneous existence of not-redness.

I claim no originality for this attempted reconciliation of the rival theories, although I am not consciously borrowing

it from another writer. The objections to it are numerous. It is psychologically crude and very incomplete. I suspect, however, that investigation along these lines might well enable a competent psychologist to reconcile the apparently opposite theories of Hering and Helmholtz, although it may reasonably be doubted whether the end would justify the trouble involved.

RECOMMENDED FOR FURTHER STUDY

The reader will find a clear account of all the important researches and a full bibliography of the subject in *A. Tschermak's* Ueber Kontrast und Irradiation (Ergebnisse d. Physiol., 1903, II. Abth., pp. 726–798).

CHAPTER XXI

THE PHYSIOLOGY OF "SPACE"

A SCIENTIFIC poet in the noble language which never failed him has set forth the conception of space as an objective reality which was once accepted by philosophers, and is still believed by those who have neither opportunity nor inclination to consider the subject with attention.[1] If, he teaches, we consider the nature of things, we find that there are bodies and empty space. Were there no empty space, bodies could have neither position nor movement. This space must likewise be intangible—

> "Cui si tactus erit quamvis levis exiguusque,
> Augmine vel grandi vel parvo denique, dum sit,
> Corporis augebit numerum summamque sequetur."

Beyond this space and the bodies moving in it nothing has existence—

> "Nam quæ cumque cluent, aut his conjuncta duabus
> Rebus ea invenies aut horum eventa videbis."

The speculations of many of the greatest philosophers of past time, pre-eminently perhaps those of Berkeley, have moulded thought into a very different form, and from the scientific side—apart from speculative metaphysics—we may be content to say that "Space and Time are not realities of the phenomenal world, but the modes under which we see things apart. They are not infinitely large nor infinitely divisible, but are essentially limited by the contents of our perception." [2]

It is, however, no part of a physiologist's business to discuss these obscure riddles. We have to recognise the existence of a faculty of separating simultaneous sense

[1] Lucretius, *De Rer. Nat.*, Bk. I., 418 *et seq.*

[2] *The Grammar of Science*, by Karl Pearson, second edition, 1900, p. 191.

impressions or, to speak rather unscientifically, of perceiving spatial relations between stimuli, and we are to inquire which of the sense organs are specially concerned in this process.

It has always been, at least in modern times, a moot point whether this power or faculty is innate or acquired, and, if the latter, which sense mechanism is to be deemed of primary importance. Without expressing any opinion at all as to which school is abstractly correct, it must be admitted that, physiologically, the work of the empiricists is of much greater importance, and the doctor of this school whose work deserves special attention is undoubtedly Berkeley. I shall, therefore, examine his views at some length.

Berkeley's contribution to the subject is contained in *An Essay towards a New Theory of Vision*, which was first published in 1709, when its author was only twenty-four years of age, being perhaps the most important contribution to modern philosophy which has been made by so young a man. Berkeley's doctrine can be summarised in a few words. Distance and magnitude are not directly determined by the nature of the images formed on the retina, nor by changes in the inclination of the optic axes. They are ideas which we form as the result of experience, and are not, strictly speaking, sensations at all.

"I know it is a received opinion that, by altering the disposition of the eyes, the mind perceives whether the angle of the optic axes, or the lateral angle comprehended between the interval of the eyes and the optic axes, are made greater or lesser; and thus, accordingly, by a kind of naural geometry, it judges the point of their intersection to be nearer or farther off. But that this is not true I am convinced by my own experience, since I am not conscious that I make any such use of the perception I have by the turn of my eyes. And for me to make these judgments, and draw these conclusions from it, without knowing that I do so, seems altogether incomprehensible."[1]

The position is defined in the following admirable passage: "From what we have shown, it is a manifest consequence

[1] Berkeley's Works, vol. i. p. 83 (Sampson's Edition, London, Bell, 1897).

that the ideas of space, outness, and things placed at a distance are not, strictly speaking, the objects of sight; they are not otherwise perceived by the eye than by the ear. Sitting in my study I hear a coach drive along the street; I look through the casement and see it; I walk out and enter it. Thus, common speech would incline one to think I heard, saw, and touched the same thing, to wit, the coach. It is nevertheless certain the ideas intromitted by each sense are widely different and distinct from each other; but having been observed constantly to go together, they are spoken of as one and the same thing. By the variation of the noise I perceive the different distances of the coach, and know that it approaches before I look out. Thus, by the ear I perceive distance just after the same manner as I do by the eye. I do not nevertheless say I hear distance in like manner as I say that I see it—the ideas perceived by hearing not being so apt to be confounded with the ideas of touch as those of sight are."[1]

The concluding sentence of this passage will suggest to the reader the weak point of Berkeley's reasoning. Although he is careful to point out that there is no necessary but only a habitual connection between visible and tangible magnitude,[2] yet in his detailed applications of the theory he is constantly accounting for visual sensations of magnitude by their connection with tangible magnitudes. Thus he concludes a discussion of units of length with the words: "From all which it is manifest that the judgments we make of the magnitudes of objects by sight are altogether in reference to their tangible extension." But there is, in theory, no reason why visual space should be subordinate to tangible space; the contrary proposition could equally well be maintained. We might, for instance, imagine that our unit of length is not a tangible impression involving some number of touch areas, but a retinal impression affecting a certain number of conoidal areas. I take it the reason why tangible magnitude is taken to be primitive is that cases of congenital blindness with normal tactile sensibility are common, while cases of total cutaneous anæsthesia of congenital origin com-

[1] *Op. cit.*, p. 98. [2] *Ibid.*, p. 102.

bined with normal vision either never occur or have never been described. It would, therefore, seem that Berkeley's treatment of the subject, admirable though it is, does not give an adequate account of spatial perception in general; its physiological importance is its insistence on a study of the empirical facts.

A somewhat similar objection has been urged by Professor James against the speculations of an even greater thinker on the subject, Helmholtz. I shall now, without further reference to the theory of the matter, enumerate the physiological data which have to be taken into consideration, beginning with the information derived from the cutaneous mechanisms.

It is a matter of common knowledge that we possess the power of localising the point of application of a tactile stimulus, and that the fineness of this power varies in different persons and in different skin areas in the same subject.

Experimentally, the matter can be investigated by the use of some form of aesthesiometer. The most useful form is an instrument constructed on the principle of a compass, the points being covered in such a way that pain is not produced by their application, and that the surface of contact with the skin is identical in both limbs. Since if two stimuli are applied together, we can when they are more than a certain distant apart recognise that two points are stimulated, and since when two different points are successively touched, we can recognise that the second stimulus was not applied to the same region as the first, two sets of experiments are to be planned. In the first set we apply the stimuli together and determine the shortest distance which corresponds to (*a*) a duplicate sensation, (*b*) a single sensation having lineal extension. In the second set the stimuli are successively employed, and we ascertain the shortest distance enabling the subject to perceive (*a*) that the second stimulated point is not identical with the first (*b*) exactly where the second point is situated. The general conclusion to be drawn from such experiments is, that the liminal distance for simultaneous is far greater than for successive stimulation. V. Frey concludes that if two neighbouring touch spots are

stimulated successively, one can always, under favourable experimental conditions, recognise that the second stimulus was not applied to the same point as the first. If the spots are touched at the same time, then a duplicate sensation does not arise, the latter being only produced if one unstimulated touch area lies between the points of application. The actual liminal distance for simultaneous stimulation varies from about 1·1 mm. on the tip of the tongue to over 65 on the upper arm or thigh. In the case of the limbs the direction of the line joining the two points is not indifferent, the liminal distance being greater for stimulation parallel with the long axis of the limb than for transverse application. The actual values obtained depend very greatly on the conditions of the experiment, the influence of fatigue being particularly apparent. Local vascular conditions also play a part, although different workers are not agreed as to their exact influence. It has also been generally asserted that practice diminishes the liminal distance, but this statement has not, I think, been entirely substantiated. That any change in the usual relations of the part stimulated greatly affects one's power of localisation is well seen in any of the modifications of Aristotle's experiment, the best being that of Henri. When the middle and ring fingers are crossed and the subject is given a diagram of the fingers in their normal relation on which he is to mark the point touched, stimuli applied to the radial side of the crossed finger tend to be localised towards the ulnar margin. Without discussing the theoretical interpretation of these results, we can pass to the visual data for space perception.

The physiological basis of spatial perception, in so far as it depends on visual sensations, is to be sought in movements of the eyes. The musculature of the eye and the exact shape of the eyeball, together with the direction and force with which each muscle pulls, have been elaborately studied. Of the methods adopted, two are of special interest.

The Method of After-images.

A coloured piece of paper is affixed to a sheet of grey paper ruled in squares of known size. The after-image of

the coloured scrap appears on different parts of the ruled surface in accordance with the way in which the eye has been moved; the ruled squares enable the position to be accurately defined.

The Substitution Method of Hering

Probably the best form of this method is that adopted by Donders in his Isoscope (Fig. 23). RR is a fixed framework on which a movable parallelogram is fixed. D is a thread attached to the frame EE, two threads attached to the parallelogram and moving with it. The parallelogram is mov-

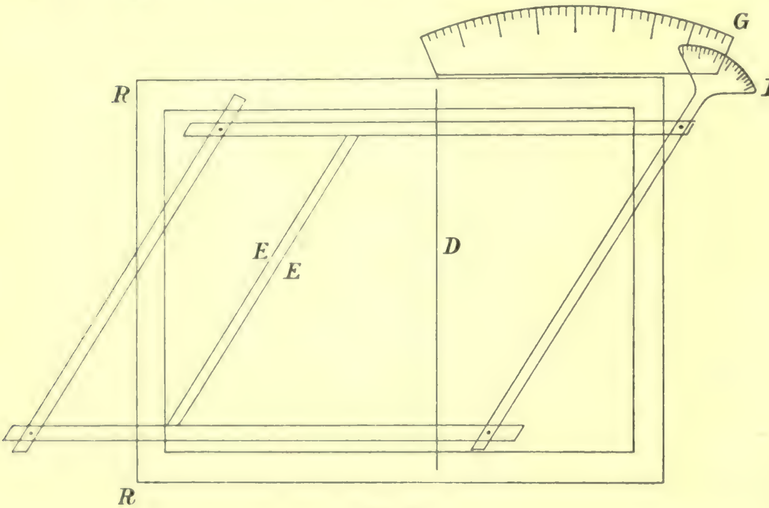


FIG. 23.

able round an antero-posterior axis, and supplied with an index pointer F reading on a scale G. With this instrument one can measure the inclination of EE and D to one another which gives parallel double images when both eyes fixate a given point. In this way one can study the apparent situation of images when the relation of the two retinæ is altered.

It is usual to call the arrangement of the eyes which obtains when the head is vertical and the visual axes parallel to the plan of the ground the "primary position." To change from this position either directly up or down or

directly to the right or the left, the eyes never rotate round an antero-posterior axis, like, for instance, the steering-wheel of a ship. The last sentence contains the teaching of Listing on this point, and is usually termed Listing's "Law." Another "Law," first propounded by Donders, is that for identical directions of the eyes the orientation of the retinæ is identical, however the eyes may have been rotated into the final position. Both these statements only apply to cases in which the visual axes are approximately parallel and movements are effected without undue muscular strain. It is of mechanical and physiological advantage for rotation to be effected in accordance with Listing's principle; the mechanical advantage is that the movement follows the shortest path and, other things being equal, can be effected in the shortest time; the physiological advantage (Hering) is that apparent rotation of an external object, owing to wheel-like movements of the eye, does not occur, and that the number of corresponding retinal points (*vide infra*) is maximal.

Numerous researches, mainly by the method of after-images, seem to demonstrate that even for parallel axes the law of Listing is not strictly true, but the deviations, at least for normal eyes, are not large.

Monocular Vision

The first question which arises is with regard to visual acuity, or the power of distinguishing between the images formed by different objects or by different parts of one object. The simplest case is an answer to the question, How far apart must two points be in order to be distinguished? The answer depends upon several circumstances, of which the most important is the amount of contrast between the points and the background (*e.g.* black points on a white surface) against which they are viewed, so that the minimum distance varies enormously in accordance with the experimental conditions. I cite a few examples on the following page.

Object.	Visual Angle.	Observer.
Parallel threads	50 secs.	Hirschmann.
Black points (on a white ground)	1 min. 4 secs.	Hueck.
White squares (on a black ground)	55 secs.	Aubert.
Parallel black lines alternating with equally broad white ones.	52 secs.–1 min. 15 secs.	Bergmann.
Jupiter's satellites	More than 2 mins.	A. Humboldt.

With good conditions of contrast and moderate illumination, Snellen's assumption that a normal eye can distinguish points separated by an angular distance of 1 minute is probably accurate enough for most purposes. Calculations made on the basis of such experiments as to the actual size of the retinal images suggest that, as in the case of touch, one unstimulated retinal element must always intervene for stimuli affecting two other elements to be separately sensed. It is generally held that, in the case of foveal vision, the retinal elements in question are the cones; whether the inner or the outer limbs of the cones are involved is a moot point, but Hensen has advanced somewhat cogent evidence in favour of the outer limbs.

For practical purposes, visual acuity at the fovea is tested by the method invented by Jäger and improved by Snellen, which is too well known to need description. The hypothesis of Snellen that the legibility of his test letters is proportional to the visual angle in every direction of the letter has not escaped question. According to Guillery, there is no uniform relation between power to recognise an object and the size of its retinal image in simple objects, and, *a fortiori*, none in the case of such complicated figures as letters. The ease with which Snellen's types can be recognised is greater than one's power of isolating the squares of a chess-board pattern seen under a visual angle of 1 minute for each square and with effective contrast. The fact is, that in reading letters of a familiar alphabet we fill in the letter mentally from seeing a small part of it, just as in a Persian

manuscript the letters are not written out in full, only the (to a native) characteristic portions of each. Snellen's method is, therefore, a test of the *minimum* of visual acuity.

Snellen's method has been modified by Cohn, who substitutes combinations of lines for the letters so that it can be used for illiterate persons. Cohn, who has investigated the normal acuity of uncivilised peoples (Beduins, Egyptians, etc.), is of opinion that the general belief that civilised peoples have lower visual acuity than uncivilised races is unfounded. His data have not, however, been submitted to rigorous statistical analysis. Cohn reports some cases of visual acuteness far transcending the normal limits; thus an Egyptian boy of sixteen had an acuity eight times the normal value, and a girl of eleven, six times the normal.

It is improbable in view of Pearson and Barrington's work that unfavourable environment—for instance, too close application to books in early childhood—is of such importance in deteriorating eyesight as various popular authors have alleged, but the subject must still be considered as of a controversial nature.

Hering has pointed out that methods such as those described, which rest on the determination of the just-noticeable distance between two objects, do not reveal the fineness of the visual "Raumsinn" for the determination of "the slightest difference in situation or magnitude which the eye can appreciate." This is analogous to the skin sense which is able to distinguish two points successively touched when closer together than two points simultaneously stimulated —*i.e.* contiguous elements of the retinal surface give rise to different sensations or have "local sign."

So far we have considered foveal acuity; as we pass towards the periphery of the retina, the acuteness of vision diminishes, under ordinary circumstances, fast, but the change is not spatially symmetrical. The falling off is more rapid in the vertical than in the horizontal meridian, and in the latter is more rapid externally than internally. Important researches on the comparative acuteness of vision in light and dark adapted eyes have been carried out by v. Kries and his pupils. V. Kries found that in dark adaptation visual

acuity between the centre of the fovea and the blind spot, at a distance of 4 to 12 degrees from the fovea, was practically constant, while at the fovea itself the test objects were imperceptible. From the blind spot outwards, acuity is the same for light and dark adapted eyes. Koester taking visual acuity as zero at the fovea ("dark" eye), found it rapidly rising at an eccentricity of 5 to 10 degrees, and from thence fairly constant towards the periphery. At an eccentricity of 30 to 40 degrees, "dark" visual acuity is greater than that of the "light" eye.

Bloom and Garten obtained somewhat different results; according to them, neither centrum nor periphery of the "dark" eye attains the degree of visual acuity possessed in light adaptation. Central and peripheral acuity are affected in the same way by dark adaptation, but not to the same extent: only when the illumination is very feeble does the dark adapted retina give the better response.

Perception of Depth with the help of one Eye

Strictly speaking, we can with the help of one eye only perceive differences of directions in lines along which points are situated, but accumulated experience enables us to distinguish depth and form with moderate accuracy. How large a part is played by past experience will be clear when we recall the numerous illusions of form which beset us when we examine distant objects for the first time. Factors which influence our judgment of relief (either in the case of monocular or binocular vision) are (1) the distribution of shadows, as seen in the fine sculpturing of snow-clad hills and valleys when the sun is low on the horizon; (2) the state of the atmosphere, aerial perspective, which causes the citizen to misjudge distances greatly when in clear mountain air.

For the judgment of the distances of near objects the state of accommodation, although of importance, does not give so much help as might be expected. Wundt has experimented on this point. The subject looks at a black thread, which can be moved nearer to or farther from a white screen, through an opening.

Although the absolute distance of the thread could not be gauged, yet, within limits, it could be ascertained in which direction the thread had been moved.

Distance of Thread.	Liminal Movement.	
	When moved Forwards.	When moved Backwards.
Metres.	Centimetres.	Centimetres.
2·5	12	12
2·2	10	12
2	8	12
1·8	8	12
1	8	11
·8	5	7
·5	4·5	6·5
·4	4·5	4·5

These experiments show sufficiently well how inexact are the data afforded by monocular vision for judging distance with the help of accommodation, and they are really too favourable, for information is afforded by changes in the brightness and distinctness of the threads. Hillebrand and others, by methods in which these latter sources of information were excluded, have found that the data afforded by changes in accommodation (or, to speak more precisely, changes in accommodation and convergence) are even less complete than Wundt's work suggests.

We all know that changes in the position of the eye—or head—with respect to the object improve our judgment of solidity. One reason why this should be so is plain. When the eye is moved the rapidity with which a retinal image changes its position depends on the distance of the object, and is inversely proportional to it. If there be two objects in the field of vision, and one moves faster than the other when the head is moved, we conclude the former to be nearer to us. Some experiments carried out by Bourdon are of interest in this connection. Two points, separated in one experiment 6 degrees, in the other 1 degree apart, were placed at about 6 metres from the eye, one point being higher than the other. The observer was allowed to move his head but not his body. In the

case of the higher point being the farther off, a correct answer was given for both distances; when the lower point was the farther off, the results were not so good but generally better for the smaller angular distances.

Judgment of Shape

This part of the subject, which includes a study of the numerous geometrical illusions, such as that of Zollner and Poggendorf, can only be dealt with in a few words. Many experiments have been performed to determine how much two straight lines must differ in order that we may perceive the difference, but the numerical values of different observers are discordant. Horizontal lines can be more accurately compared than vertical ones, and a comparison of horizontal and vertical distances leads to still greater errors. If one attempts to draw a square on a plane at right angles to the line of sight, the vertical sides may be as much as one-fifth shorter than the horizontal ones, the least error being one-sixtieth to one-thirtieth. According to Feilchenfeld, when a rectangular cross is approximated to the eye one increasingly over-estimates the nasal limb, a result which he attributes to the greater extent of the temporal visual field. If one freely chooses the fixation point in monocular vision, the temporal half of a line to be bisected is over-estimated because (Feilchenfeld) the point which lies along the fixation line, and is too much towards the temporal side, is erroneously taken to be the centre. These explanations appear to me to leave the experimental facts pretty much where they were before.

The various ways in which the eye can be deceived with regard to form and direction are too well known through the medium of popular magazines to need reproduction, and I confine myself to a diagram of the Müller-Lyer illusion (Fig. 24). The part of the horizontal line towards which the short lines approach appears shorter than the exactly equal portion from which the lines recede. Painstaking attempts have been made to interpret this and similar illusions, with indifferent success. Some regard the basis

as directly sensational, others as secondary or dependent upon a process of subconscious or unconscious inference.

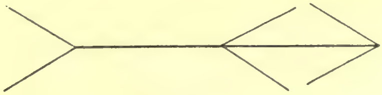


FIG. 24.

Helmholtz has interpreted many of these illusions on the basis of a "law of contrast," according to which clearly perceived differences are judged to be greater than indistinctly perceived ones, a reversal of the old dictum, *omne ignotum pro magnifico.* He explains in this way the well-known illusion that a distance divided by dots appears greater than the same space not divided, the former being more distinctly seen, and therefore judged to be greater. In other cases, irradiation and ocular movements are thought to be influential.

Hering has suggested that the apparent distance between two points depends on the linear distance of their retinal image points. Hence, small distances are more accurately judged than large ones, since the length of the chord of a small arc approximates to that of the arc. Einthoven attributes certain illusions to differences of distinctness between images formed at the fovea and on the peripheral retina. It may, perhaps, be said that since our knowledge of all the factors which are involved in judgment of size is, even at the physiological level, imperfect, the explanations put forward are rather of interest as intellectual exercises than as complete interpretations of the phenomena. One interesting problem must be mentioned, viz. the reason why the moon on the horizon looks larger than when she is at the zenith, a question which has been touched on by such proficients as Berkeley, Gauss, and Helmholtz. The experiments of Zoth appear to prove that the influence of aerial perspective, of the comparison with objects of known size, and of the apparent curvature of the sky, are not the main determining factors in the illusion. Zoth holds that the apparently smaller size of the moon at the zenith depends on the necessary elevation of the eye. Guttman's experiments, which demonstrate an

apparent diminution in size of $3\frac{1}{2}$ to $3\frac{2}{3}$ per cent. in objects 25 to 36 cm. distant placed so that the line of vision has an elevation of 40 degrees, confirm this view, but only push the difficulty one stage farther back. The association of upward gaze and diminution in size may possibly be due to the convergence which occurs when the eyes look upwards (Zoth).

Binocular Vision

The most obvious advantage of using both eyes is the increased power we notice of observing the solidity of objects, but before we examine the physiological basis of this we must consider some of the data which help us to understand the joint working of the eyes. Since whenever we turn our eyes to a point a separate image of it is formed on each retina, it is a remarkable thing that we see not two points, but one only.

This remarkable and, so far as we are concerned, ultimate fact can be expressed by the statement that the retinæ contain areas or points which "correspond," viz. the simultaneous excitation of which calls up a single sensation. We also know that when the ordinary mutual arrangement of the eyes is disturbed, *e.g.* by pushing one eyeball with the finger, a single object gives rise to two images. Hence, any two retinal areas do not indifferently "correspond"; some retinal points are disparate. The first problem is, accordingly, to determine how the "corresponding" points lie with reference to some fixed retinal point taken as origin, or, in other words, to map out the binocular field of single vision.

The locus of the external points, images of which fall on "corresponding" points of the two retina, is called the Horopter, or, more strictly, the Point Horopter, and it can be investigated in numerous ways. Theoretically, it might seem an easy task to map out the horopter experimentally; a point might be fixed and a small object moved round on a perimeter, the positions being noted in which it was seen as a single point or as two points. Again, a haploscopic arrangement can be used, mirrors capable of rotation on different axes being adapted to the purpose. Unfortunately these ex-

periments are very difficult to carry out; they require a highly trained subject as well as an experienced observer, for recognition of double images (diplopia) is only easy in extreme cases. It has, therefore, been more usual to determine the horopter theoretically, using a few simple experimental data as a starting point. The data used are the following:—

Simple observation appears to show that symmetrical points of the two retinæ "correspond," *e.g.* that when a point on the right retina 1 millimetre to the left of the fovea in the horizontal meridian and a point 1 millimetre to the left of the left fovea in the same meridian are stimulated, that a single image is seen. Accepting this datum, the problem reduces itself to finding the locus of external points, the images of which are formed on symmetrical areas of the retina and becomes purely geometrical. The geometrical problem is indeed somewhat complex, because *inter alia* the eyes can be moved in so many directions, but it is one which a highly skilled geometer could solve without ever leaving his study. It will be observed that two assumptions are made in stating the problem in this form, viz. (1) the stimulation of symmetrical points is always attended by single vision; (2) the stimulation of asymmetrical points does not call up a single image. Of these assumptions, (1) is probably but not certainly true, (2) is almost certainly false. It thus follows that the geometrical horopter does not correspond accurately to the physiological one, but it is true that the divergence is not, so far as we know, very considerable. I do not think, however, that I should be justified in reproducing the difficult investigation by which the theoretical horopter has been obtained, and it is possible that even a statement of its results will not be quite clear to all readers. Helmholtz found that the point horopter is in general a curve of double curvature, and can be regarded as the section of two surfaces of the second order, which have in addition a common straight line. In a particular case only is the point horopter a plane surface, viz. when the fixation point lies at infinity in the mesial plane, and the horizontal meridia of the retinæ are in the visual plane. Under these conditions the horopteric plane is either perpendicular to the line of sight and at

infinity, or parallel to the visual plane and passes through the line of intersection of the planes of the apparently vertical meridian; for normal eyes the line of section and the horopteric plane nearly coincide with the plane of the ground on which the observer stands. When we consider not points but lines the problem becomes still more complex, and cannot be even summarised in an elementary treatise.

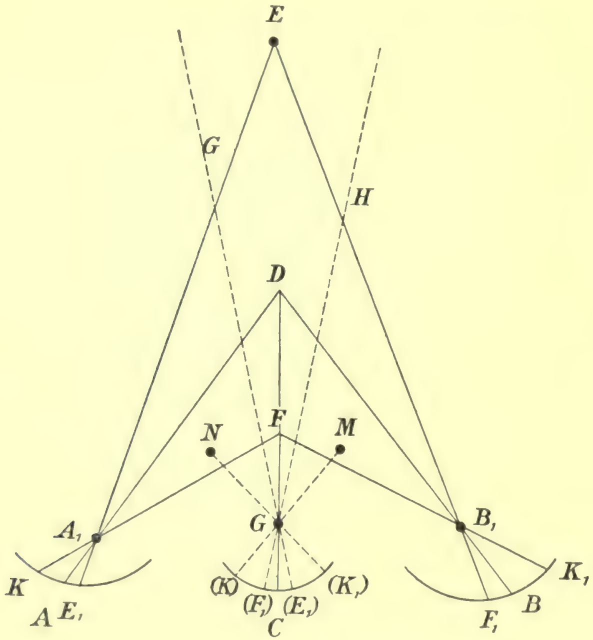


FIG. 25.

We must now touch on the rules which appear to govern the projection of objects viewed with both eyes. The most important empirical law is that worked out by Hering, and is very simple to understand.

Let A and B represent the right and left eyes, and A_1 and B_1 their nodal points, C an imaginary "cyclopean" eye, and C_1 its nodal point. Let D be the point to which the eyes converge, so that its images are formed on corresponding points. Join DA_1, DB_1, and DC_1, and produce to intersect

the retinæ. Then the point D appears along the line DC_1. In a similar way the localisation of double images is clear.[1]

We now come to the factors which render the two eyes working together more efficient than the separate organs for discriminating sizes. Of these, convergence and binocular parallax are the most important. With regard to the former, the experiments of Wundt, Bourdon, and others appear to justify the following statement: Convergence affords a better means of measuring distance than do changes in the state of

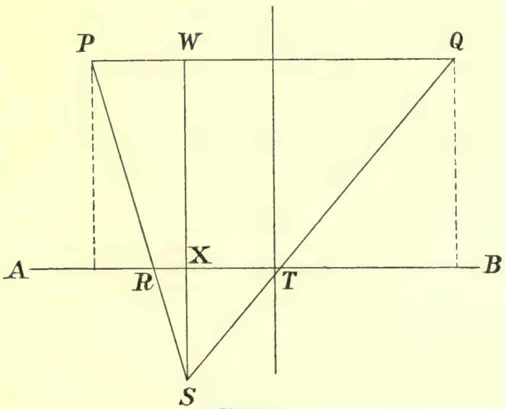


FIG. 26.

accommodation, yet the information so obtained does not rank in importance with that due to parallax.

The importance of parallax, the apparent difference in an object viewed from two different points in the special case of binocular vision, was first described by Wheatstone in 1838. Let AB (Fig. 26) be the horizontal section of a plane at right angles to the plane of the paper, which we will regard as the visual plane, P and Q the mid-points of the lines of vision of the two eyes, and S a point looked at. R and T are the projections of S on AB. Let a be the distance between the eyes and c the distance from R to T, b the distance

[1] When D is fixated, the images of the point E are formed at E_1 and F_1. (F_1) and (E_1) are the points which correspond to F_1 and E_1 upon the Cyclopean Retina. Join (F_1) and (E_1) to G and produce to intersect EF_1 and EE_1. The image due to the right eye is projected along $(F_1)H$, *i.e.* there is *Uncrossed Diplopia.* In a similar way, we find the image of the nearer point F due to the right eye is projected to the left—*Crossed Diplopia.*

of AB from PQ, f the distance from S to PQ, and d the distance from S to AB.

Since the triangles PSQ and RST are similar,

$$\frac{c}{d}=\frac{a}{f} \text{ and } c=\frac{ad}{f}.$$

$a-c=e$, can be called the stereoscopic distance (Helmholtz). Further,

$$\frac{b}{d}=\frac{a-c}{c} \text{ or } e=\frac{bc}{d}=\frac{ba}{f}.$$

Both c and e diminish when f increases, and vanish when f is infinite; in other words, there is no binocular parallax for very distant objects. Both c and e increase with the interocular distances, c increases as the distance of the object from the plane of projection, e as the distance of the projection plane from the eyes.

Many experimental determinations of the fineness of depth perception have been carried out. Helmholtz measured how far the central one of three needles must be moved

Bourdon's Experiments on Judgment of Distance.

[The Plane of the Fixed Needles was 2 meters from the Eyes.]

[The Needles were 35 mm. apart.]

Position of the Middle Needle.		Results of Twenty Trials.		
		" Nearer."	" The same Distance."	" Farther."
In front of the others	3·0	20	0	0
	2·5	20	0	0
	2·0	19	1	0
	1·5	18	2	0
	1·0	17	3	0
	·5	11	9	0
	·0	2	18	0
Behind the others	·5	3	15	2
	1·0	0	13	7
	1·5	0	11	9
	2·0	0	3	17
	2·5	0	0	20
	3·0	0	1	19

forwards or backwards for a difference to be noticed. He found that a needle 34 centimetres from the eyes when

moved through half a millimetre, approximately its thickness, backwards or forwards from the plane of the others, could be detected with certainty as being no longer in that plane. Bourdon's experiments reveal even greater accuracy. Calculation on the basis of Bourdon's work shows that a difference in position of the retinal images corresponding to five angular seconds is appreciable. In ordinary observation of a solid body we are accustomed to change the fixation point frequently, and it has been thought that these eye movements are of great importance in spatial perception. It is, however, fairly certain that although such movements are not without value, their importance in comparison with binocular parallax is secondary.

Stereoscopy

I shall conclude this chapter with a few words descriptive of a matter which, although not a part of the physiology of visible space, is germane to it, viz. the theory of the stereoscope.

If it be true that binocular parallax is the main foundation of what we call solidity or depth, it should follow that when two pictures of an object taken from the point of view of each eye are so presented to the binocular combination that the images are made to fuse, an impression of solidity is produced. This deduction, first made by Wheatstone, has been the foundation of optical experiments which have produced instruments of great interest and practical use.

Photographic pictures for stereoscopy are taken with objectives somewhat farther apart than the average distance between the eyes, and accordingly represent such effects as would be produced naturally by rather nearer objects than those which they represent, *i.e.* there is an exaggeration of the relief. Owing to the fact that the observed points lie in a plane, the state of accommodation associated with the convergence of the optic axes is not quite appropriate; there is not a complete reproduction of the natural state of affairs. To unite the two pictures Wheatstone employed an arrangement of mirrors, but Brewster's device of two prisms (Fig. 27) has

proved more satisfactory. The older instruments were mostly box-shaped, light being admitted through a slit in the front wall, but these have been largely replaced

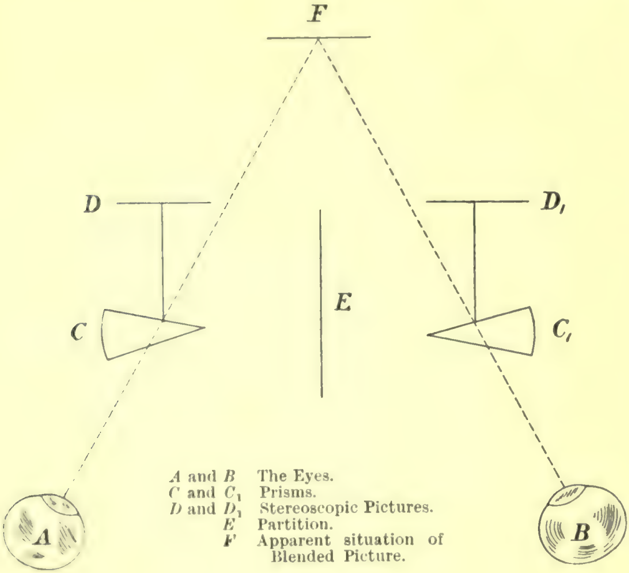


FIG. 27.

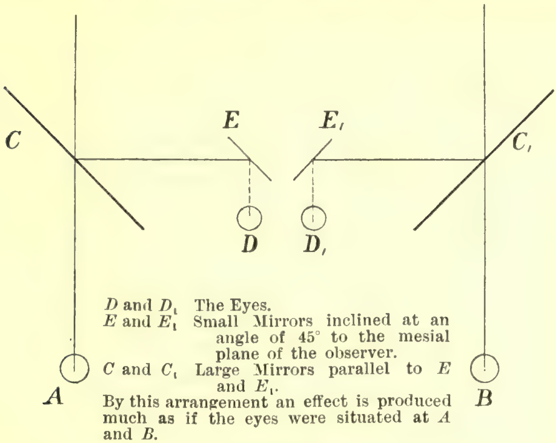
by open instruments, such as the admirable hand stereoscope of the Zeiss works.

Very useful applications of the stereoscope have resulted from modifications of the distance between the eyes; the principle of one of these is shown in the diagram (Fig. 28).

Supposing, now, that one places in the image planes of a binocular telescope two glass plates with a series of corresponding signs, in accordance with the ocular distance (modified by and a constant of the instrument); some object is fixated, and one notices at which point in the series of marks it is seen stereoscopically. Each of the pairs of marks corresponds to a definite distance (depending on the corrected ocular distance), and in this way the distance of the object can be directly read off. This is the principle of the Stereotelemeter made by Zeiss; the accuracy of their smaller

instrument is ± 5 cm. for a distance of 20 metres, $\pm 31 \cdot 3$ m. for 500 metres. Their larger instrument reads to 440 m. in 10 kilometres.

If two absolutely identical pictures or impressions on a plane surface are examined with a stereoscope, the fused impression, as we should expect, is once more that of a flat surface. If, however, the two patterns are not absolutely



D and D_1 The Eyes.
E and E_1 Small Mirrors inclined at an angle of 45° to the mesial plane of the observer.
C and C_1 Large Mirrors parallel to E and E_1.
By this arrangement an effect is produced much as if the eyes were situated at A and B.

FIG. 28.

identical, then, in accordance with the principles of stereoscopic vision an imperfect appearance of relief, an obliquely vaulted image is obtained. Medals stamped with the same die but from different metals, although indistinguishable to touch or by the naked eye, have been found to produce this effect (Dove); different editions of printed books and forged bank-notes can also be detected in this way. For such purposes, a modified stereoscope, Pulfrich's Stereocomparator, has been introduced with satisfactory results; indeed, the adaptations and modifications of Wheatstone's instrument are numerous, and will in time be more so.

The brief sketch presented in this chapter will, perhaps, help the reader to form an idea of the diverse fields of intellectual research which are touched on by the physiological study of spatial magnitude; he will find that almost any of the branches of inquiry which each part of the subject

suggests can be made the source of great pleasure and instruction.

RECOMMENDED FOR FURTHER STUDY

(1) The masterly article on Space in the second volume of *Professor William James'* Principles of Psychology should first be mastered. Next come (2) *Helmholtz's* treatise, and (3) *Hering's* article in Hermann's Handb. d. Phys., Bk. iii. part 1. (4) An admirable summary of the physiological data relating to visual space is given in *Zoth's* article in Nagel's Handb., vol. iii.

INDEX

THE END

Printed by Ballantyne, Hanson & Co.
Edinburgh & London

# Mr. Edward Arnold's List
OF
MEDICAL BOOKS.

Further Advances in Physiology.

Edited by LEONARD HILL, M.B., F.R.S.

With Contributions from Professor BENJAMIN MOORE, University of Liverpool; MARTIN FLACK, B.A., M.B., Oxon.; LEONARD HILL, M.B., Lecturer on Physiology, London Hospital; Dr. THOMAS LEWIS; Dr. ARTHUR KEITH, Curator of the Hunterian Museum, Royal College of Surgeons; Dr. M. S. PEMBREY, Lecturer on Physiology, Guy's Hospital; Dr. N. ALCOCK, Lecturer on Physiology, St. Mary's Hospital; Dr. JOSEPH SHAW BOLTON; MAJOR GREENWOOD, M.R.C.S., Director of Statistical Department, London Hospital.

448 pages. With Diagrams and Index. Demy 8vo. 15s. net.

Recent Advances in Physiology and Bio-Chemistry.

Edited by LEONARD HILL, M.B., F.R.S.

Contributors:

BENJAMIN MOORE, M.A., D.Sc.; LEONARD HILL, M.B., F.R.S.; J. J. R. MACLEOD, M.B., Professor of Physiology, Western Reserve University, Cleveland, U.S.A.; late Demonstrator of Physiology, the London Hospital; M. S. PEMBREY, MA., M.D.; and A. P. BEDDARD, M.A., M.D., Assistant Physician, late Demonstrator of Physiology, Guy's Hospital.

xii + 740 pages. With Diagrams. Demy 8vo., cloth, 18s. net.

Practical Physiology.

By A. P. BEDDARD, M.A., M.D.; J. S. EDKINS, M.A., M.B.; LEONARD HILL, M.B., F.R.S.; J. J. R. MACLEOD, M.B.; and M. S. PEMBREY, M.A., M.D.

Second Edition.

xvi + 503 pages. With Illustrations. Demy 8vo., cloth, 12s. 6d. net.

From the LANCET.

"We can assure the student that, armed with the knowledge that he will acquire by sedulously following the scheme of work laid down for him in orderly fashion in addition to his usual studies, he will be well equipped for the examination of patients and the diagnosis of disease. The application of the facts that are given, if thoroughly understood, will be the work of his life in the sick-room, and will distinguish him from the (sometimes misnamed) practical but imperfectly educated man."

London: EDWARD ARNOLD, 41 & 43 Maddox St., Bond St., W.

Human Embryology and Morphology.

By ARTHUR KEITH, M.D. Aberd., F.R.C.S. Eng.,

Lecturer on Anatomy, London Hospital Medical College; formerly Hunterian Professor, Royal College of Surgeons, England, Examiner in Anatomy, University of Aberdeen, and in the Natural Science Tripos, University of Cambridge.

Second Edition. Revised and Enlarged.

xii + 402 pages, with 316 Illustrations in the text, of which 64 are new in this edition. Demy 8vo., cloth, 12s. 6d. net.

Applied Physiology.

A Handbook for Students of Medicine.

By ROBERT HUTCHISON, M.D. Edin., F.R.C.P.,

Physician to the London Hospital and Assistant Physician to the Hospital for Sick Children.

Crown 8vo. Price 7s. 6d. net.

Lectures on Diseases of Children.

By ROBERT HUTCHISON, M.D. Edin., F.R.C.P.

New and Enlarged Edition.

xii + 428 pages. With 64 Illustrations. Crown 8vo., cloth, 8s. 6d. net.

Manual of Human Physiology.

By LEONARD HILL, M.B., F.R.S.,

Lecturer on Physiology, London Hospital Medical School; Hunterian Professor, Royal College of Surgeons; Examiner in Physiology for the Conjoint Board of the Royal Colleges of Physicians and Surgeons.

xii + 484 pages, with 173 Illustrations. Crown 8vo., cloth, 6s.

The Physiological Action of Drugs.

An Introduction to Practical Pharmacology.

By M. S. PEMBREY, M.A., M.D.,

Lecturer on Physiology, Guy's Hospital:

and C. D. F. PHILLIPS, M.D., LL.D.,

Examiner in Materia Medica and Therapeutics in the University of Aberdeen, late Examiner in the Universities of Edinburgh and Glasgow.

With 68 Diagrams and Tracings. Demy 8vo., cloth, 4s. 6d. net.

The Diagnosis of Nervous Diseases.

By PURVES STUART, M.A., M.D., F.R.C.P.,

Physician to Out-Patients at the Westminster Hospital; Joint-Lecturer on Medicine in the Medical School; Physician to the Royal National Orthopædic Hospital; Assistant Physician to the Italian Hospital.

New Edition, Revised and Enlarged.

450 pages. With Illustrations from the Author's Photographs, and Coloured Plates. Demy 8vo., 15s. net.

A Guide to the Diseases of the Nose and Throat, and their Treatment.

BY CHARLES A. PARKER, F.R.C.S. EDIN.,
Surgeon to the Throat Hospital, Golden Square, W.

xii + 624 pages. With 254 Illustrations. Demy 8vo., cloth, 18s. net.

Movable Kidney: its Pathology, Symptoms, and Treatment.

BY H. W. WILSON, M.B., B.S. LOND., F.R.C.S. ENG.,
Demonstrator of Anatomy, St. Bartholomew's Hospital;

AND

C. M. HINDS HOWELL, M.A., M.B., M.R.C.P., LOND.,
Junior Demonstrator of Physiology, St. Bartholomew's Hospital.

Demy 8vo., 4s. 6d. net.

A Handbook of Skin Diseases and their Treatment.

BY ARTHUR WHITFIELD, M.D. LOND., F.R.C.P.,
Professor of Dermatology at King's College; Physician to the Skin Departments, King's College and the Great Northern Central Hospitals.

xii + 320 pages. With Illustrations. Crown 8vo., 8s. 6d. net.

A Manual of Pharmacology for Students.

BY WALTER E. DIXON, M.A. CANTAB., M.D., B.S., B.SC. LOND., D.P.H. CAMB.,
Assistant to the Downing Professor of Medicine in the University of Cambridge; Examiner in Pharmacology in the Universities of Cambridge and Glasgow.

xii + 451 pages. With Illustrations. Demy 8vo., cloth, 15s. net.

The Laws of Health.

BY D. NABARRO, M.D., B.SC., D.P.H.,
Assistant Professor of Pathology and Bacteriology, University College, College, London.

viii + 184 pages. With Illustrations. Crown 8vo., cloth, 1s. 6d.

The Body at Work.

BY ALEX HILL, M.A., M.D.,
Recently Master of Downing College, Cambridge; Author of "An Introduction to Science," etc.

With Illustrations. Demy 8vo., 16s. net.

Food and the Principles of Dietetics.

By ROBERT HUTCHISON, M.D. Edin., F.R.C.P.,

Physician to the London Hospital and Assistant-Physician to the Hospital for Sick Children, Great Ormond Street.

xx + 582 pages, with 3 Plates in Colour and 34 Illustrations in the text. Demy 8vo., red buckram, 16s. net.

The Influence of Alcohol and other Drugs on Fatigue.

By W. H. RIVERS, M.D., F.R.C.P., F.R.S.,

Lecturer in Physiological and Experimental Psychology at Cambridge University.

Royal 8vo., 6s. net.

The Chemical Investigation of Gastric and Intestinal Diseases by the Aid of Test Meals.

By VAUGHAN HARLEY, M.D., Edin., M.R.C.P., F.C.S.,

Professor of Pathological Chemistry, University College, London;

and FRANCIS GOODBODY, M.D., Dubl., M R.C.P.,

Assistant-Professor of Pathological Chemistry, University College, London.

Demy 8vo., 8s. 6d. net.

BOOKS FOR NURSES.

Surgical Nursing and the Principles of Surgery for Nurses.

By RUSSELL HOWARD, M.B., M.S., F.R.C.S.,

Lecturer on Surgical Nursing to the Probationers of the London Hospital.

With Illustrations. Crown 8vo., 6s.

Midwifery for Nurses.

By HENRY RUSSELL ANDREWS, M.D., B.Sc., Lond., M.R.C.P. Lond.,

Examiner to the Central Midwives Board.

New Edition. With Illustrations. Crown 8vo., 4s. 6d. net.

A Text-Book of Nursing.

By C. S. WEEKS-SHAW.

Revised and largely Rewritten by W. Radford, Senior Resident Medical Officer, Poplar Hospital.

xiv + 344 pages. With numerous Illustrations. 3s. 6d.

UNIVERSITY OF TORONTO
LIBRARY

Do not
remove
the card
from this
Pocket.

Acme Library Card Pocket
Under Pat. "Ref. Index File."
Made by LIBRARY BUREAU, Boston

Author Greenwood, M. (Junior) 104475 m Phy G.
Title Physiology of the Special Senses